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TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

VOL. 105

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7
1954

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON, LIMITED,
BARTHOLOMEW PRESS,
DORKING, SURREY.

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Vol. 105. Part 1. Pp. 1–10. 7 plates 15th April, 1954

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PUBLISHED BY THE SOCIETY AND
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EVOLUTIONARY TRENDS IN THE THYNNINAE (HYMENOPTERA: TIPHIIDAE) WITH SPECIAL REFERENCE TO FEEDING HABITS OF AUSTRALIAN SPECIES.

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Manuscript received 30th July, 1953.
(Read 4th November, 1953.)

With 7 Line Plates.

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Introduction.

During the period December, 1945, to April, 1952, while engaged on a search in Australia for parasites suitable for use against the melolonthid pasture scarab *Costelytra zealandica* (White) in New Zealand, the author paid considerable attention to wasps of the subfamily Thynninae (family Tiphiidae). Some 14,000 pairs of these wasps, representing 13 species, were consigned to New Zealand. Species were designated by index number as no comprehensive named reference collection exists in Australia, and on attempting to identify the species consigned at the termination of the project, it was found that on existing keys and descriptions many species could not be satisfactorily placed even to generic status. The impression gained is that the keys of Turner (1907–1910) are somewhat artificial in their construction, and that further research is necessary as a basis for a natural classification of the group. However, although Turner himself indicated that a reclassification of the subfamily might be required on the accumulation of further data and material, his observations, keys and descriptions are of considerable value. Many of his observations on the phylogeny of the group have proved to be correct (e.g., the genus *Glyptometopa*, then known from females only, he considered possibly to have a *Brachycistis*-like male (1910). It has now been proved (Mickel and Krombien, 1942) that the corresponding male is a brachycistidine). The earlier keys of Ashmead (1903) were basic to Turner's work, but it was the latter who gave us our present concept of the subfamily (then family).

Pate (1947) reviews the tiphiid complex, placing the sub-family Tiphiidae with 7 other subfamilies. Following on this, it is logical to reduce Turner's subfamilies Diamminae, Rhagigasterinae and Thynninae to tribal status. This has been done in the present paper.

Since Turner's generic keys (1910) were found to be unsatisfactory, and considerable field knowledge of the group has been gained during the past few years, the author has been prompted to carry out the present study. This is a preliminary account which it is hoped will stimulate further observation and investigation in Australia and South America, in which countries the subfamily principally occurs. Knowledge of the subfamily is not yet satisfactory for systematic purposes and it is highly desirable that trends and modifications herein described be added to by future workers, until the peculiar specialisations and affinities of this important group become clarified.

Technique and Limitations of Figures.

For the general series of figures representing entire heads, no special treatment was used, heads being removed from normal dried cabinet specimens and mounted on card strips beneath specimens. For lateral views of entire heads with mouthparts extended, material was treated in hot 10 per cent caustic potash solution and drawn while under water. To retain the heads in the correct position for drawing, a pin, bent to an L-shape, was inserted into the foramen. In the drawing of female mouthparts, material treated in hot caustic potash and permanently mounted on slides was used in most cases.

The postero-ventral figures of male heads (Plate IV) were drawn for the purpose of illustrating the extension of the concave area and should not be considered as accurately displaying other outlines or structures. The marginal fringe of hairs is illustrated only where it forms a definite food-holding structure, other vestiture being omitted. This also applies to the labiomaxillary lateral profile figures.

In the figures of female labiomaxillary structures, all vestiture is omitted from the series on Plate V, and outlines are somewhat diagrammatic. As far as possible, the maxillae are represented to illustrate their greatest breadth but parted apically to show clearly the labial palpal bases. This position is quite unnatural in many cases. Figures on Plate V do not illustrate any of the glossae or other apical elements except the palpi.

In no case except in Plate III are sizes of figures strictly relative, and figures on Plate VII representing feeding attitudes are purely diagrammatic.

The More Obvious Evolutionary Trends.

It is generally considered by present-day workers that the more primitive form of the family Tiphiidae is represented by the genera completely winged in both sexes (*Tiphia*, *Anthobosca*, etc.). In accordance with the requirements created by fossorial host search, the greatest degree of structural modification is probably evident in the Thynninae and Brachycistidinae, and it is the Thynninae which is the most successful of the apterous groups.

The most obvious modification in accordance with fossorial habit is the reduction of wings culminating in complete absence in the females of Thynninae and some other subfamilies. Both sexes being nectar or honey-dew feeders, the requirement of transport for females between food source and oviposition site produces modification along one of two lines:

(*a*) Development of legs of female for rapid ambulation, and
(*b*) development of the copulatory mechanism of both sexes to serve in coupling for transport by males.

The first of these developments is exemplified by *Diamma bicolor* Westwood, in which species legs of females are well developed for running, but are not such efficient digging organs, allowing of entry into friable soils only, or entry by means of burrows of other insects. The female of *Diamma* has well developed eyes, functional ocelli, and normal mouthparts and genitalia in accordance with its free-feeding habit and ground mating.

It has been generally assumed that all members of the Thynninae except *Diamma bicolor* fly coupled and it has been surmised that in all such cases females are transported to feeding areas in this way. However, this assumption is not strictly correct, although short nuptial flights may be general. In all cases (except *Diamma*), however, females appear to be dependent on males for food. The serving of this function is along three known lines: (*a*) Males feeding females by regurgitation. (*b*) Males storing food in concave excavations beneath the head and usually transporting food to the waiting females. (*c*) Free-feeding females carried to food-source by males. Within these three groups, surprising modifications of habit and structure are evident, and undoubtedly much still remains to be observed and interpreted.

Before considering in some detail these three highly specialised lines of modification, general modifications associated with the transport-dependence of females are worthy of mention. In the females, reduction of eyes and elimination of ocelli are very evident, although in some species traces of ocelli appear to be present but never functional except in *Diamma*. Reduction of body size and size of antennae and palpi, considerable modification of legs to serve a burrowing function, development of great strength in genital and pre-genital segments, and the development of a variety of carinae, rugosity, etc., on dorsal abdominal plates to aid in passage through the soil, are much in evidence in females. Mandibular modification to serve in clasping the male and protection of mouthparts is also apparent. In males, the only general modifications are in development of flight mechanism and genital claspers and associated organs, although some remarkable modifications of mouthparts occur in more highly specialised genera.

FEEDING-HABITS.

No accurate observations of any extent have been published on the feeding-habits of the Australian Thynninae, and, in the literature available, few data on these habits have been found concerning the South American forms.

Burrell (1935) observed the more primitive feeding habits of members of the Rhagigasterini, and appears to have assumed that other groups behave similarly. Turner (1910*a*) records observations made by Giles in Western Australia, who noted regurgitation in some species. However, the mechanism of this regurgitation has not hitherto been recorded. From dissection and inspection of mouthparts of females, it would appear that South American forms are more primitive than those of Australia, being self-feeding in both sexes (Plate I, fig. 3).

As mentioned above, three major categories have been observed in method of female feeding. These will be dealt with in some detail in the following remarks under the headings already indicated.

(a) *Feeding by Regurgitation* (Plate VII, figs. 2–5, 7).

This is almost certainly the dominant method of female feeding in the Thynninae of Australia. In general, the females are transported to the feeding area which may be blossom, scale infestation, aphid infestation, jassid colonies, or extra-floral nectaries. Males feed for some minutes, retire to secluded places such as the under-sides of leaves, and feed the females. Several different modifications of the actual method of food-transfer have been observed, and these are as follows:

(1) Direct regurgitation (mouth to mouth) with female held ventro-medially (Plate VII, fig. 3).

(2) Direct regurgitation with female held ventro-laterally (Plate VII, fig. 2).

(3) Food regurgitation on to ultimate abdominal segments of male, where it is accessible to female in normal transport position. In this type of feeding, the male usually does not retire from food source to feed female (Plate VII, fig. 4).

(4) Regurgitation on to leaf or petal surface, and lateral swinging of female to reach food droplet deposited (Plate VII, fig. 5).

In all feeding by regurgitation observed, it has appeared necessary for the mouthparts of the female to be completely immersed in feeding solution. In cases of mouth to mouth feeding, the males extrude moderately large droplets which are held between the palpi, para-glossae and glossae, fringes of long hairs on the stipites, or in various other ways in the vicinity of the mouthparts. The female head is frequently half immersed in this droplet during feeding, and when the droplet is largely transferred, her head is withdrawn and both sexes proceed to absorb the remains of the liquid. In larger species, the contraction of the food globule is readily observed, and the efficiency of the process is surprising. Little trace of external nectar is to be seen on a female killed immediately after feeding. In the case of regurgitation on to ventral abdominal segments the droplet is again large, and frequently the entire ventral and part of the dorsal surface of the female is bathed in liquid, yet contraction of the globule on feeding by the female leaves little trace of liquid on body surfaces. The process of feeding is essentially similar in the case of species the males of which deposit droplets on leaf surfaces, etc. This last group are mostly feeders on scale exudations.

Although the majority of males of species falling into this group transport females to food sources, this is not universal. A notable exception is *Hemithyn-*

nus apterus (Oliver), the male of which is rarely if ever to be seen transporting its female.

It is possible that some species combine the regurgitation method with that of sub-occipital storage.

(b) *Feeding from Sub-occipital Storage.*

The male head in this group is deeply excavated beneath (Plate II, figs. 1–2) and into this excavation, nectar (frequently from extra-floral nectaries) or more often honey-dew from scales, is deposited. The mechanism of this storage has not been worked out in detail, but is a very rapid process. In many species the final food bolus, held in place by a fringe of long recurved hairs is considerably larger than the head, which is itself considerably larger than in the more typical genera (Plate VII, figs. 6, 7).

In many species which have this feeding habit, particularly the more highly specialised of the group, females are never transported to the food source, and in many cases are rarely seen. In some species of the genus *Tachynomyia*, which represents the highest degree of evolution of the food-storage head in males, females frequently cling to males by mandibles only, even when in flight, and are often not attached by the genital organs when feeding.

(c) *Self-feeding females* (Plate VII, fig. 1).

Under this heading, females self-feeding while attached to males are considered. This self-feeding habit while coupled is mainly (in Australia) a characteristic of the genera *Rhagigaster* and probably *Dimorphothynnus*. Some of the species which are normally fed by regurgitation will in rare cases feed themselves when the natural food supply occurs in sufficiently large deposits, as at some scale infestations.

In this group, the male disposes itself to give the maximum coverage of the food-source to the female, and the elongate abdomen in each sex further increases this range. In *Rhagigaster*, the female mouthparts are very well developed, while in the allied *Eirone* a range from rudimentary to moderately well developed structures occurs.

STRUCTURAL MODIFICATION OF MOUTHPARTS.

Although at first investigation the most striking modification is in the reduction of the female mouthparts with progressive dependence on the male (Plates I, III), further study shows more significance in the specialisation of male structures (Plates II, IV, VI). From the normal unmodified rhagigasterine mouthparts, male structures show progressive specialisation through regurgitation in the presence of droplet-holding recurved hairs on the maxillae and mandibles, to the excavated head with greatly elongated recurved marginal hairs, and densely haired labium and palpi (Plate II, figs. 1–3). The development of these structures and the homology of the excavation will be dealt with in the following section of this paper.

In the females, reduction of mouthparts is naturally somewhat parallel to development of both regurgitation feeding and feeding from sub-occipital storage. Reduction in size of the labiomaxillary parts is the first obvious modification, followed by reduction in structural development of glossal elements and palpi. From the fully-developed structures with 6 maxillary and 4 labial palpal joints, reduction has been noted to structures with no true glossae, 0 maxillary and 1 labial palpal joint, with the lacinia and galea reduced on either side to a lightly chitinised, feebly-spinose ridge (Plates V, VI). Further, in the females the mandibles show a degree of modification to serve a clasping function. In *Rhagigaster*, where they are not much used in clasping the male, the space enclosed between mandibles and clypeus when the former are meeting tip to tip is insufficient to hold the male at the base of the parameres (Plate I, fig. 5), whereas in those species which retain a mandibular grip during transport, this space is suited to the size and shape of the bases of the male sexual structures (Plate I, fig. 6).

Further modification in the mandibular structure serves to protect the mouthparts during burrowing. As will be seen from Plate I, fig. 7, the mandibles when completely closed overlap to form an almost perfect barrier across the more delicate labiomaxillary structures, and this protection is further improved by the presence of strong bristles on the lower clypeal margin and labrum (which folds over glossae and palpal bases when mouthparts are retracted), and strong posteroventral fringes of bristles on the mandibles. The submentum and stipites, when retracted, present an almost flat heavily chitinised surface continuous with the lower surface of the head.

THE EVOLUTION OF THE EXCAVATED HEAD IN THE MALES.

The excavated head of the genus *Tachynomyia* is the structural culmination of an evolutionary trend in feeding mechanics and the extent of living links occurring in the chain of developmental phases should give the subfamily Thynninae in Australia a claim to further attention by those interested in basic problems of evolution.

The homological study of this excavation indicates that the entire area is derived from the suture or margin of the labiomaxillary fossa, and it should be noted that in *Tiphia* this area is somewhat broadened (Plate II, fig. 5), indicating a potential flexibility in primitive members of the family Tiphiidae. The broadening of this margin can be readily traced as illustrated on Plate IV. Undoubtedly, this broadening, flattening, and later concavity was primarily of assistance in holding larger droplets of food than could be held within the glossae and maxillary bristles alone, and as larger areas became excavated, the need for internal storage and regurgitation became less, feeding economy of effort was reduced with increased storage space, until the peak of development in *Tachynomia* species 20 was reached. It may be pointed out that the figures on Plate IV represent only selected intermediates extant in the series of excavation expansion. A complete series from all known species would provide a chain of closer affinity.

It is of interest to note that, in many species, males of this genus rarely carry females to the food source, and the nearer perfection the food-storage mechanism, the less frequently are females carried. (In the case of *Tachynomyia* sp. 20, although thousands of males were seen during collecting operations at Wannon, near Hamilton in Victoria, no females were ever seen or taken, despite surveys covering a radius of several miles from the focus of feeding.) This means an obvious economy of time for female activity, which may thus be confined to the breeding-ground, while the males provide complete transport for food.

In parallel with the expansion of the labiomaxillary fossa margin, a development of recurved maxillary hairs is noted, followed by their reduction as a submental " beard " appears. The recurved hairs at the margins of the excavation increase in development throughout, and, in the final stages of development of the genus *Tachynomyia*, interesting modifications became apparent in the labial palpi (Plate IV, figs. 10–12). The basal joint first becomes somewhat elbowed to allow the remaining ones to protrude free of the food globule, and, at the same time, this basal joint develops a fringe of elongate hairs which aids in confinement of the food. In the final stage (Plate IV, fig. 12) the basal joint is broad and flattened, with a great development of the marginal fringe, and with the second joint inserted on a papilla near the centre of its outer surface.

The homology of the excavation to the margin of the labio-maxillary fossa is obvious from the figures given and this homology is further supported by the fact that the entire area is absolutely devoid of sculpture or vestiture. In *Tachynomyia* sp. 20, even the occipital area is smoothly concave, but this area, unlike the major concavity, is finely punctured, and bears a fringe of hairs.

OTHER MALE HEAD MODIFICATIONS.

There are several types of head which are modified along lines different from those described above. The writer recognises from material at his disposal, such modifications in the following genera :

(a) *Megalothynnus.*

In this genus the male head is somewhat depressed ventrally and bears long fringing hairs on genae and mandibles. However, the genus is not known from personal field observation, and therefore feeding habits cannot be discussed. The female has somewhat reduced mouthparts, but with the full number of palpal joints of somewhat modified structure (Plate V, fig. 13).

(b) *Oncorrhinus.*

Males with ventrolateral excavated areas on the head not united, and with the maxillary bases folded to form a tubular channel opening basiventrally between excavations. Feeding is probably by regurgitation. Female mouthparts typically reduced with palpal formula of 4 : 1 (labial palpal joints : maxillary palpal joints).

(c) *Zeleboria* ?.

Three species of this genus were present in collections studied, and of these one has been observed feeding by regurgitation. Male heads are figured on Plate VI. In the figures, the margin of the labiomaxillary fossa of the male is drawn black, and the stippled area is completely unpigmented chitin. In fig. 3 the male head is represented with mouthparts extended. When the mouthparts are retracted, instead of the stipites folding back on a simple basal articulation, they retreat downward and back so that the recurved hairs illustrated are mostly behind the unpigmented plate, through which they may be clearly seen. It would appear that this vitreous plate is derived from outward growth from either side of the lower margins of the fossa, and its unpigmented nature and the fact that it is only partly fused at its median junction, indicates it to be a comparatively recent development.

REDUCTION OF FEMALE MOUTHPARTS (Plates V, VI)

The greatest degree of reduction appears to be in the regurgitation feeders, and the peak is reached in the rather aberrant species figured on Plate VI. The majority of species, apart from those whose females are self-feeding, fall into the palpal formulae 4 : 3, 4 : 2, 4 : 1, and 3 : 2 (Table I).

TABLE I.—*Distribution of numbers of species examined to palpal formulae.*

		Number of joints in maxillary palpi.						
		6	5	4	3	2	1	0
Number of joints in labial palpi	4	15	1	.	7	10	6	.
	3	.	.	.	1	6	1	1
	2	.	.	.	.	1	1	.
	1	.	.	.	.	.	2	1
	0	.	.	.	.	.	.	.

Reduction is primarily in maxillary palpi, and secondarily in labial palpi; variation is frequently noted within genera, although in the only three species of the genus *Agriomyia* examined, a remarkable constancy was noted in both number and form of palpal elements, despite the fact that the species were not closely allied (Plate V, fig. 15).

The degree of reduction of typical female mouthparts in regurgitation species is illustrated in Plate III, in which male and female structures are drawn to scale.

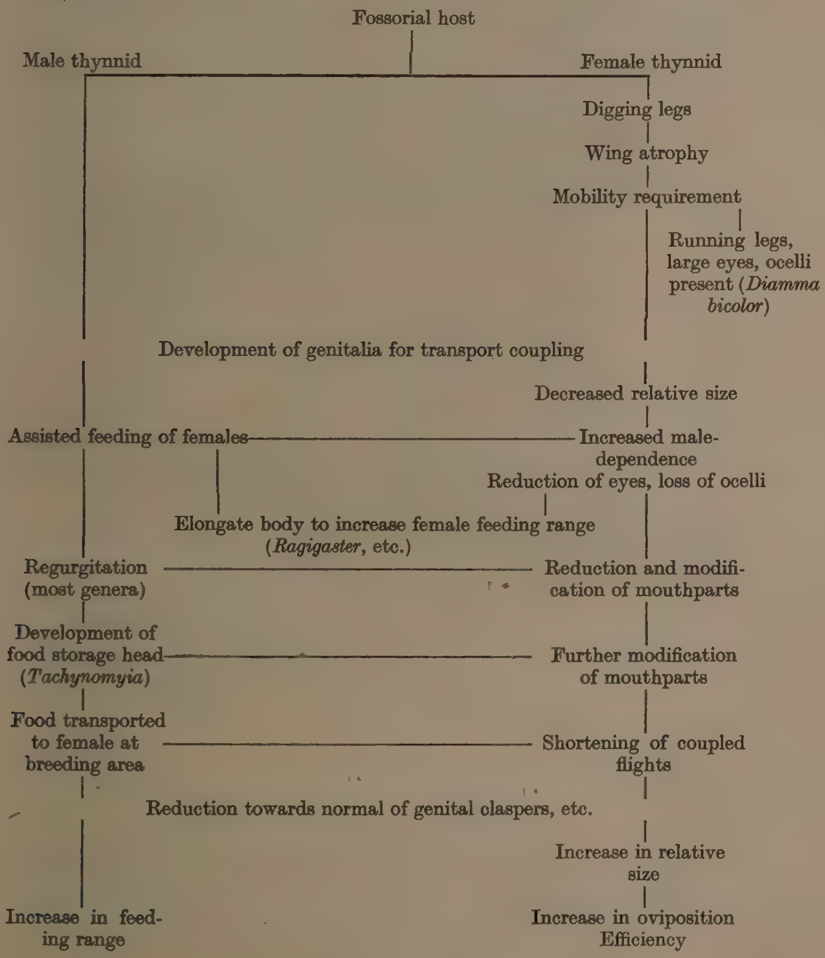
CONCLUSIONS AND DISCUSSION.

The Tiphiidae are generally considered to be a primitive family of the Hymenoptera, and are rarely considered among the more highly evolved and specialised groups. Perhaps the foregoing remarks which touch on the fringe of one rather restricted though large subfamily may help to dispel this fallacy. In some regards no doubt these insects are primitive, but their diversity of habit and form and their success in the area which they inhabit proves them able to adapt themselves to the changing environment, and this adaptability is further proven by the establishment of at least one species in an adopted country on an adopted host (Given, 1953). It may be said that lack of host specificity is itself a primitive character. It may also be said that adaptability is a pre-requisite for success in the struggle for existence, and in the Thynninae there are both highly specific and rather diffuse host relationships. It is at least certain that over large areas of Australia the Thynninae are (apart from the Formicidae) the dominant macrohymenopterous group.

At the most recent period when the South American and Australian sections of the group were separated, it is doubtful if the specialisation of feeding habits and structures herein described had commenced, since there is no evidence of their occurrence among the South American elements.

It is of interest and importance to note that the genus *Tachynomyia*, which illustrates the remarkable development of the male food-storage head, occurs in New Guinea. Species of this genus whose habits are known, are parasitic on larvae of Melolonthinae and Aphodiinae in Australia, and do not carry females any distance. Hence it seems unlikely that the occurrence of the genus in New Guinea has resulted from any natural cause other than a land connection between the two countries. On the other hand, as evidence points to the fact that the structure of the head of *Tachynomia* has developed from some primitive type of regurgitation feeding mechanism, it seems strange that no such regurgitating species should have been collected in New Guinea or New Caledonia, where the genus *Eirone* (self-feeding in both sexes) occurs.

The following chart represents in diagrammatic form the evolution of the feeding habits of the Thynninae, and consequent structural modification.


Fossorial host
Male thynnid
Female thynnid
Digging legs
Wing atrophy
Mobility requirement
Running legs, large eyes, ocelli present (*Diamma bicolor*)
Development of genitalia for transport coupling
Decreased relative size
Assisted feeding of females
Increased male-dependence
Reduction of eyes, loss of ocelli
Elongate body to increase female feeding range (*Ragigaster*, etc.)
Regurgitation (most genera)
Reduction and modification of mouthparts
Development of food storage head (*Tachynomyia*)
Further modification of mouthparts
Food transported to female at breeding area
Shortening of coupled flights
Reduction towards normal of genital claspers, etc.
Increase in relative size
Increase in feeding range
Increase in oviposition Efficiency

From the systematic point of view, it is obvious that the shape and extent of the ventral concave areas on the heads of males of the more highly specialised Thynninae can be of considerable value. The mouthparts of the females are more difficult to utilise, as in many cases it is necessary to dissect and examine the structures under relatively high magnification in order to determine the number of joints in the maxillary palpi. The genera *Ariphron*, *Tachynomyia* and *Agriomyia*, as well as several monotypic or very small genera, can be very readily identified by the male head concavities, and the absence of these features at once separates off the *Rhagigasterini*, probably all South American genera, *Thynnus* and *Megalothynnus*.

SUMMARY.

The more obvious evolutionary trends of the Thynninae are briefly discussed and diagrammatically illustrated, as a contribution to a better understanding of the affinities of members of the subfamily. Particular stress is laid on the peculiar habits involved in female feeding and related structural modification of the mouthparts and heads of both sexes. Both regurgitation and self-feeding processes are described; the evolution of the excavated male head of the genus *Tachynomia* is illustrated and the homologies of the various areas involved demonstrated. In addition, several aberrant forms are mentioned and in conclusion mention is made of the remarkable success of the group and of the age of their specialisation of habit and structure.

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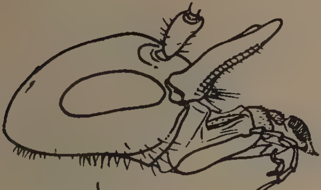
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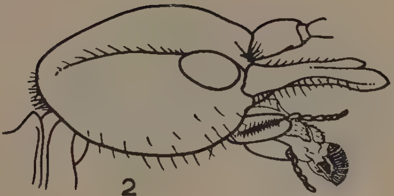
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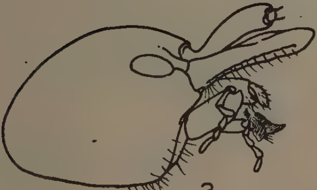
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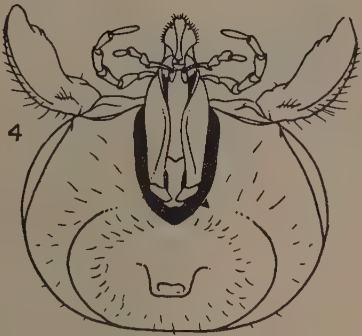
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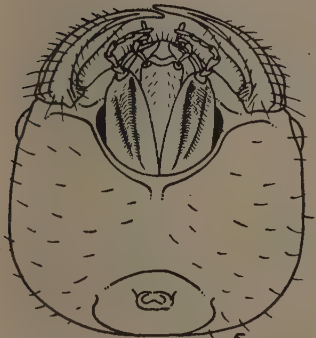
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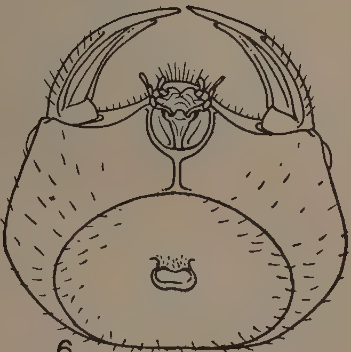
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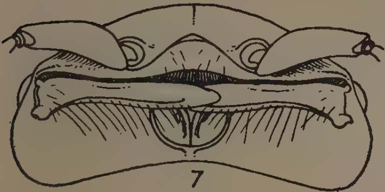
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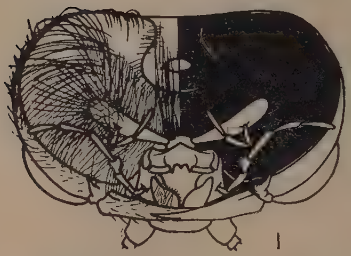
FIGS. 1–3.—Head lateral, mouthparts extended, of (1) *Diamma bicolor*, ♀; (2) *Rhagigaster*, sp. K.1, ♀; (3) *Elaphroptera scoliaeformis*, ♀.
FIG. 4.—*Diamma bicolor*, ♀, head ventral, mouthparts extended.
FIG. 5.—*Rhagigaster*, sp. K.1, ♀, head ventral, mouthparts partly extended.
FIG. 6.—*Tachynomyia*, sp. 69, ♀, head ventral, mouthparts partly extended.
FIG. 7.—Sp. 66, ♀, head anterior, mouthparts retracted.



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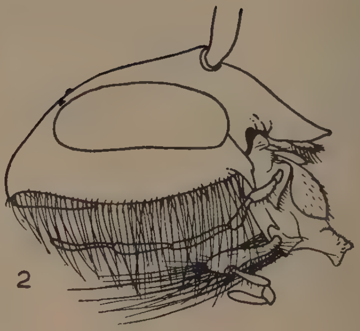

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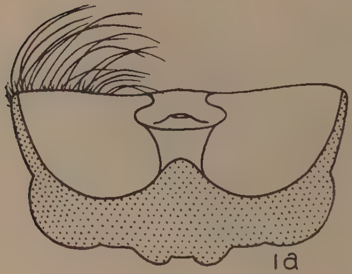

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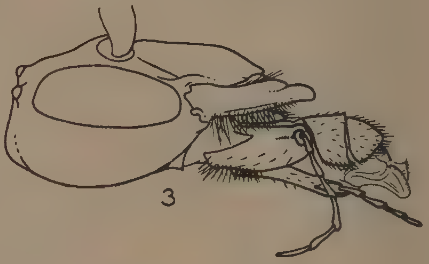

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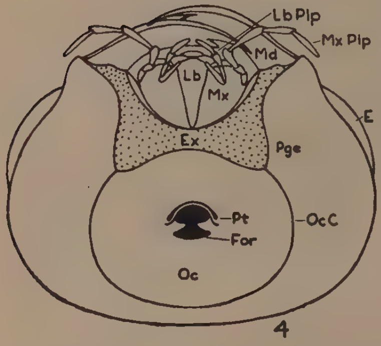

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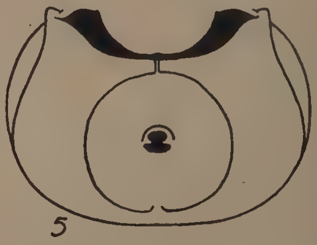

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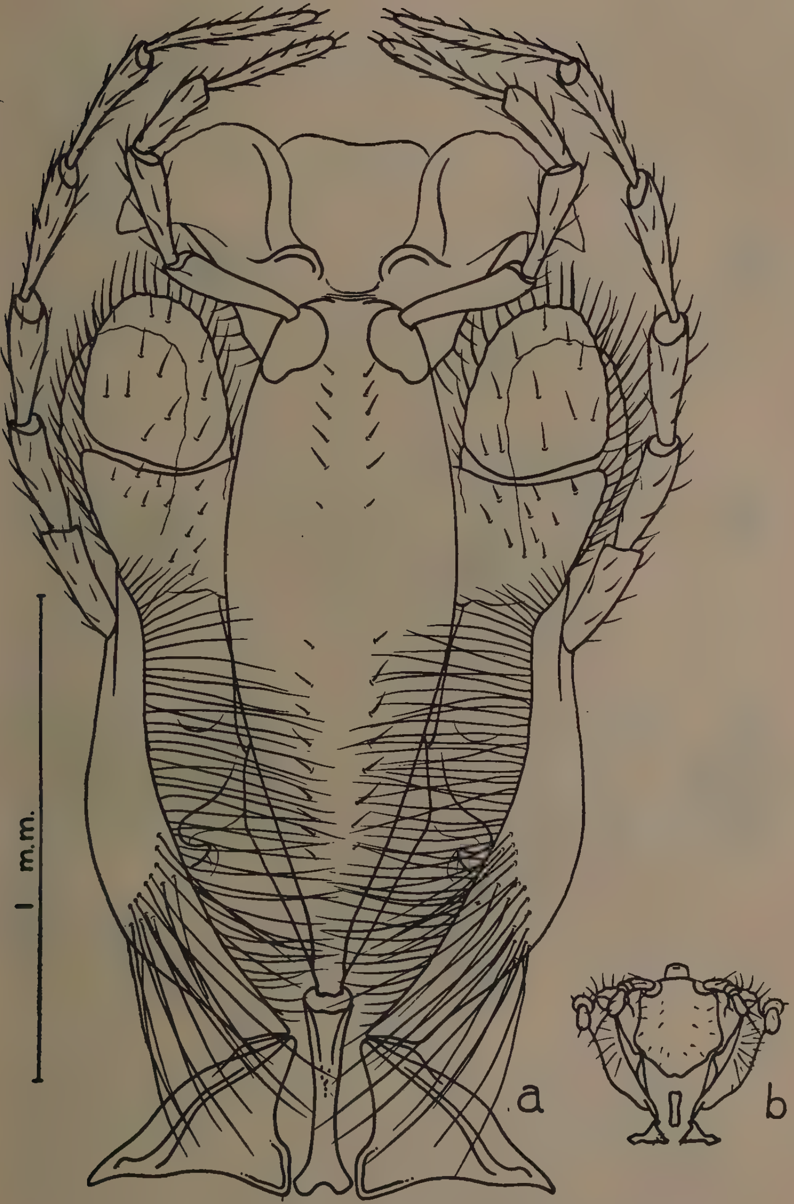
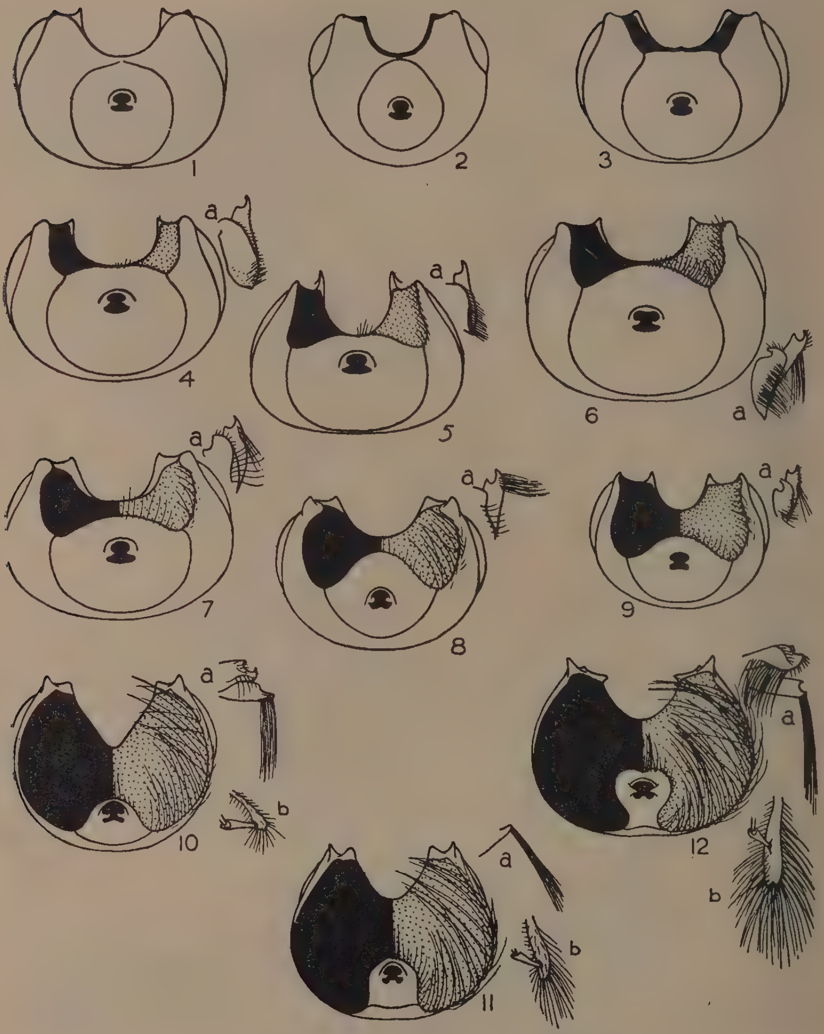
FIG. 1.—*Tachynomyia*, sp. 20, ♂, head ventral, concave areas of right side black, with vestiture removed.
FIG. 1*a*.—*Tachynomyia*, sp. 20, ♂, head section to illustrate depth of concavity.
FIG. 2.—*Tachynomyia pilosula*, ♂, head lateral, mouthparts extended (mandibles removed).
FIG. 3.—*Hemithynnus apterus*, ♂, head lateral, mouthparts extended.
FIG. 4.—*Ariphron bicolor*, ♂, head ventral.
FIG. 5.—*Tiphia vernalis*, ♂, head capsule, ventral.

Key to lettering.

E = Eye ; *Ex* = Expanded margin of labiomaxillary fossa ; *For* = Foramen ; *Lb* = Labium ; *LbPlp* = Labial palp ; *Md* = Mandible ; *Mx* = Maxilla ; *MxPlp* = Maxillary palp ; *Oc* = Occiput ; *OcC* = Occipital carina ; *Pge* = Paragena ; *Pt* = Posterior tentorial pit.



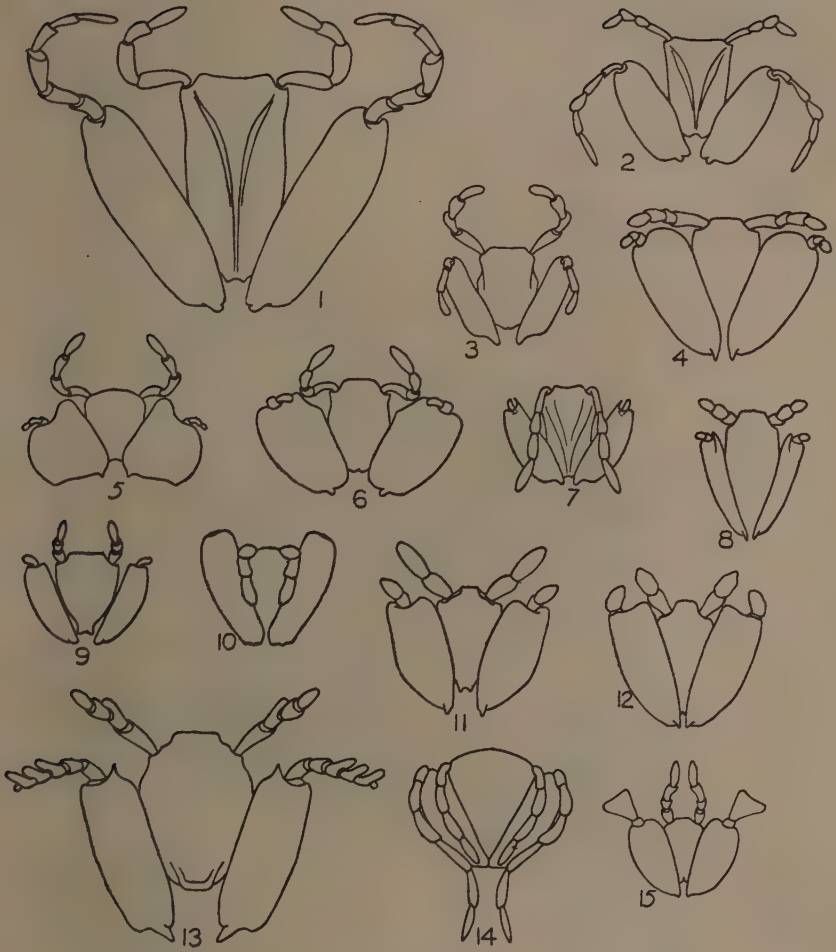
Thymnoides gracilis. (?). (*a*) ♂, mouthparts ; (*b*) ♀, mouthparts.



(Illustrating evolution of sub-occipital cavity in male thynnids.)

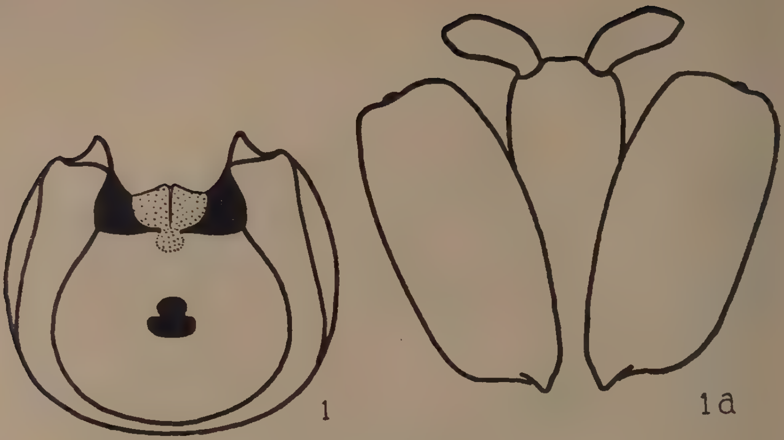
Figs. 1–3.—Head capsule, ventral, of (1) *Eirone*, sp. 73, ♂; (2) *Rhagigaster*, sp. K.1. ♂; (3) *Agriomyia*, sp. 94, ♂.

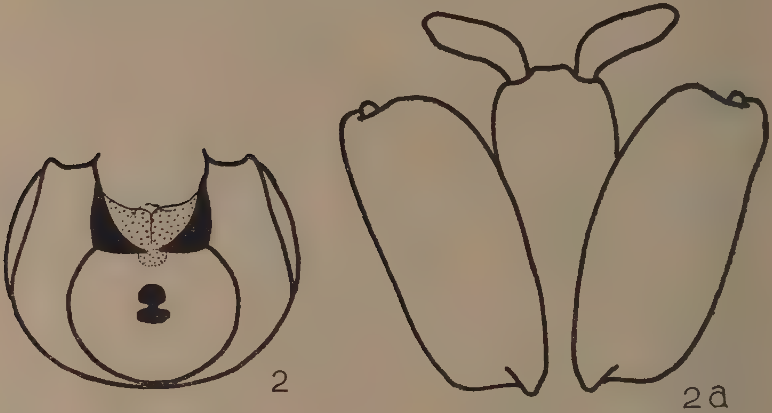
Figs. 4–12.—Head capsule, ventral, and (*a*) labiomaxillary profile of: (4) *Lestrichothynnus frauenfeldianus*, ♂; (5) *Zaspilothynnus carbonarius*, ♂; (6) Sp. 17, ♂; (7) Sp. 66, ♂; (8) Sp. 46, ♂; (9) *Asthenothynnus*, sp., ♂; (10) *Tachynomyia senex*, ♂; (11) *Tachynomyia pilosula*, ♂; (12) *Tachynomyia*, sp. 20, ♂.

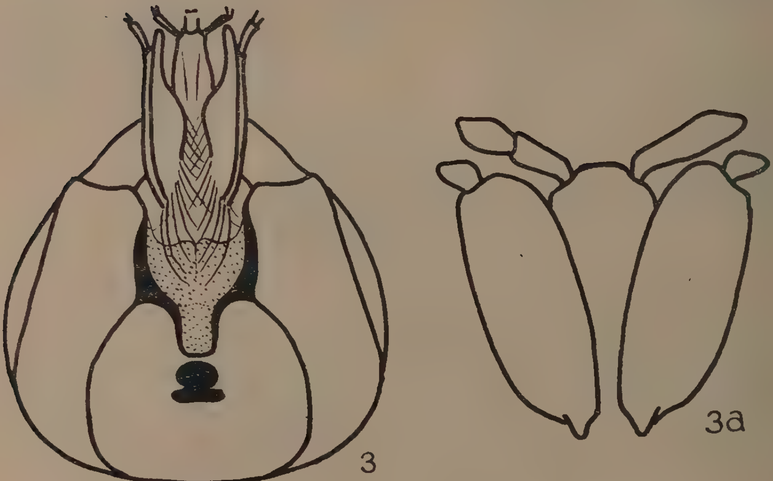


(Illustrating reduction in maxillary and labial palpi in female thynnids.)

FIGS. 1–15.—Mouthparts of: (1) *Rhagigaster*, sp. K.1, ♀; (2) *Rhagigaster*, Sp. 28, ♀; (3) *Eirone*, Sp. 73, ♀; (4) *Zaspilothynnus hackeri*, ♀; (5) *Tachynomyia rubella*, ♀; (6) Sp. 46, ♀; (7) *Ariphron tryphonoides*, ♀; (8) *Zaspilothynnus carbonarius*, ♀; (9) *Aeolothynnus*, sp. 26, ♀; (10) Sp. 41, ♀; (11) Sp. 50, ♀; (12) Sp. 49, ♀; (13) *Megalothynnus klugii*, ♀; (14) *Tiphia vernalis*, ♀; (15) *Agriomyia luctuosus*, ♀.

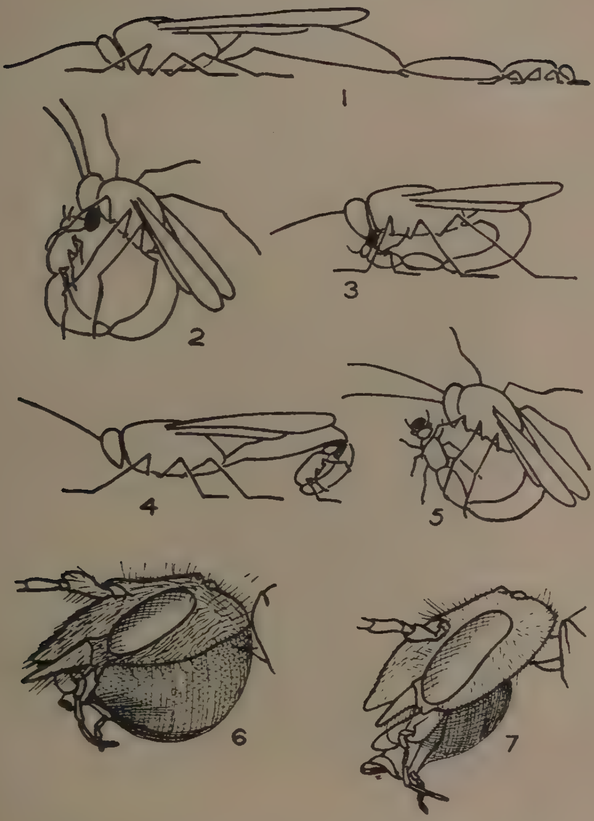






(Head modifications in certain aberrant forms (*Zeleboria ?*).)

Fig. 1.—Sp. A. 9, ♂, head capsule, ventral ; (*a*) ♀, mouthparts.
Fig. 2.—*Zeleboria marginalis*, ♂, head capsule, ventral ; (*a*) ♀, mouthparts.
Fig. 3.—Sp. 56, ♂, head, ventral ; (*a*) ♀, mouthparts (left labial palp abnormal).



(Feeding attitudes and carriage of food droplets by males.)

Fig. 1.—Rhagigasterine female feeding attitude.
Fig. 2.—Female feeding attitude of spp. 66, 46, and 2.
Fig. 3.—Female feeding attitude of sp. 11 and sometimes 46.
Fig. 4.—Female feeding attitude of sp. 24.
Fig. 5.—Female feeding attitude of spp. 24 and 25.
Fig. 6.—Position and size of food droplet carried by *Tachynomyia*.
Fig. 7.—Position and size of regurgitated droplet on *Thynnoides gracilis* (?).

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THE METHOD AND IMPORTANCE OF THE RECOGNITION BY A COLONY OF HONEYBEES (*A. MELLIFERA*) OF THE PRESENCE OF ITS QUEEN.

By C. G. Butler, M.A., Ph.D., F.R.E.S.

(*Bee Research Department, Rothamsted Experimental Station.*)

Manuscript received 7th August, 1953.

(Read 4th November, 1953.)

With 1 Text-figure.

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Introduction.

When a colony of honeybees loses its queen the worker bees soon become aware of the fact (often within thirty minutes or less) and the behaviour of the colony as a whole tends to change from a state of organised activity to one of disorganised restlessness. If the hive of a colony that has recently lost its queen is opened many of the bees expose their scent producing (Nassanoff) glands and fan currents of air over them with their wings, thus producing the "roaring" sound which is associated with queenlessness. Within a few hours a more definite sign of queenlessness becomes apparent, as one or more worker brood cells containing young female larvae will usually have been modified by the bees to form emergency queen cells. The larva in one of these cells is destined, all being well, to become the new queen of the colony.

So quickly do the bees of a colony become aware of the absence of their queen that it seems impossible to believe that each bee can make contact with its queen often enough to remain aware of her presence (i.e., every thirty minutes or so). One is, therefore, led to suppose that the bees of a colony are normally kept aware of the presence of their queen either directly, as might be the case if she were to emit some specific queen odour which permeates the hive atmosphere and is appreciated by all the bees; or, indirectly, by those bees which have recently been in contact with their queen somehow informing other members of their colony of this fact, this information being passed from bee to bee at frequent intervals.

Müssbichler (1952) accepts the latter view, basing her conclusion on the results of some experiments in which she found that when she caged a queen honeybee amongst a group of her own workers these bees did not exhibit any signs of queenlessness provided that they could actually make contact with their queen. She also found that when contact between a queen and a group of her workers is interrupted by a space, these bees soon exhibit signs of queenlessness whether or not the space which separates them from their queen is filled with bees.

The work described in this paper indicates that whilst Müssbichler's conclusion is substantially correct it cannot be satisfactorily based upon results of the experiments which she describes, as these results are not necessarily obtained when her experiments are repeated. In fact it has been found possible to obtain results which seem, at first sight, to render Müssbichler's hypothesis untenable. However, the following results not only strongly support the view that the worker bees of a colony do inform each other of the presence of their queen but also demonstrate the means by which such information is conveyed from bee to bee.

Experiments with Cages.

The bees of colonies headed by actively laying queens free to move amongst their workers do not normally construct emergency queen cells, nor do they tolerate the presence of such cells if they are introduced into their colonies by beekeepers. It was desirable, therefore, to determine what conditions (other than queenlessness) result in bees constructing emergency queen cells. Laying queens were caged, or had their freedom of movement restricted in some other way, so that the free association of the queen with her workers was limited to a predetermined extent. The degree of separation between a queen and her workers varied from almost normal free association to complete separation, apart from sight and possibly hearing of one another and perhaps of some odour from the queen or workers which might have diffused into the hive atmosphere.

Four distinct methods of restricting a queen's movements were employed: (*a*) The queen was confined in a cage with walls made of a single thickness of wire-gauze (3 mm. mesh). (*b*) The queen was placed in a cage with walls made of two thicknesses of wire-gauze, separated from one another by a space 1·25 cm. wide. (*c*) The queen was confined in a cage with walls of queen-excluder (i.e., perforated zinc, with perforations in the form of long slots through which workers, but not queen nor drone, honeybees could readily pass). (*d*) The queen was attached to a vertical wooden board within the hive so that she could not walk about, but in such a way that her bees had direct access to any predetermined part of her body.

Bees outside the single-walled cages could feed and have considerable contact with any bees inside them and were observed to do so, but when double-walled cages were used such contact was impossible. When the queen-excluder cages were used bees, other than the queen, could pass freely in and out of them and were seen to do so.

In each experiment the laying queen of a colony was taken and caged (or attached to a board), usually together with a small number of her own workers, on comb containing a supply of pollen and honey, so that she was only separated from the rest of the members of her colony by the wall of the cage. After forty-eight hours the colony was thoroughly examined for emergency queen cells, the presence of even one of which was adopted as a criterion of queenlessness. The results obtained are shown in Table I.

TABLE I.—*Effects of caging laying queens in various ways on the production of emergency queen cells in colonies of various strengths.*

A. *With colonies containing at least* 8000 *adult worker bees, a few workers present in each cage with queen. Food present in all cages.*

Type of cage.	Times used.	Times emergency queen cells formed.
None. Queen attached to wooden board	8	0
Perforated zinc cage through walls of which workers could pass	8	0
Single-walled wire-gauze	13	13
Double-walled wire-gauze	5	5

B. *With colonies containing not more than* 2500 *adult worker bees, a few workers present in each cage with queen. Food present in all cages.*

Type of cage.	Times used.	Times emergency queen cells formed.
Perforated zinc cage through walls of which workers could pass	4	0
Single-walled wire-gauze	6	2
Double-walled wire gauze	5	5

C. *With colonies containing at least* 8000 *adult worker bees, no workers present in cage with queen, food in double-walled cage but none in single-walled.*

Type of cage.	Times used.	Times emergency queen cells formed.
Single-walled wire-gauze	4	4
Double-walled wire-gauze	3	3

It is clear from these results that the sight of their queen together with any odour from her body which may reach them is insufficient to prevent worker honeybees from constructing emergency queen cells.

The data also indicate that when the bees of a colony, containing 8000 or more adults, were able to approach closely to the body of their queen (tethered or queen-excluder cage) they did not build any emergency queen cells. If, on the other hand, the bees of colonies of this size were prevented from making direct contact with their queens (double-walled cages), or the amount of contact they could make was limited (single-walled cages), then emergency queen cells were soon built. It should be noted that the bees did make regular contact with their queens when the latter were confined in single-walled cages, as the queens survived in such cages even when no bees nor food were provided in them, which they could not have done unless they were fed by bees outside the cages.

However, when the queens of very small colonies (less than 2500 adults) were caged in queen-excluder cages, or in single-walled wire-gauze cages, their workers did not as a rule build emergency queen cells, although they did so in every case when their queens were confined in double-walled cages.

These results strongly suggest that the worker bees of a colony, or at any rate the household bees, obtain from their queen regular supplies of some substance which inhibits them from building emergency queen cells, and that it is necessary for the bees to have physical contact with their queen in order to obtain this " queen substance." Furthermore, since the bees of colonies containing more than 8000 adult workers built emergency queen cells when their queens were in single-walled cages through which the bees made some contact with their queens, whereas the bees of very small colonies did not tend to do so, it appears that it is necessary for any given number of bees to acquire a certain minimum amount of " queen substance " in order that they shall remain inhibited from building emergency queen cells. In fact, whereas a given amount of " queen substance " will " satisfy " a small number of bees it may be insufficient to " satisfy " a larger number.

However, it seems improbable, especially in the case of a large colony, that every worker bee obtains a share of " queen substance " by direct contact with her queen. It seems more probable that only a certain limited number of bees obtain this substance directly from the queen and that they then share it out amongst the other members of their colony.

Two types of experiments were carried out to check this point.

EXPERIMENTS TO DETERMINE WHETHER WORKER HONEYBEES ARE ABLE TO "INFORM" OTHER MEMBERS OF THEIR COLONY OF THE CONTINUED PRESENCE OF THEIR QUEEN.

A large colony of bees was taken during July, 1952, and divided into three parts or nuclei. One nucleus (A) consisted of twelve combs, six of which contained brood, together with adult bees and the queen. The other two nuclei (B and C) were approximately equal in strength. Each consisted of five combs, three of which contained brood including very young worker larvae suitable for rearing as emergency queens, and between 3000–4000 adult bees but, of course, no queen. Each nucleus was housed in a separate, well-ventilated hive and the bees were prevented from flying.

Ten minutes after the colony had been divided up, twenty worker bees were taken at random from the tops of the frames of nucleus A—the queen-right nucleus—and were introduced into nucleus B. Thereafter, every five minutes twenty bees were taken from nucleus A and introduced into nucleus B. No bees were added to nucleus C which served as a control. Once every hour nuclei B and C were examined carefully for any signs of emergency queen cell construction. Any bees which escaped during these examinations flew away and were ignored. Three hours after the experiment was started the bees in nucleus C, the control nucleus, were behaving in a queenless manner and it was thought that three worker cells containing young larvae were being modified as emergency queen cells, but the observer was not absolutely certain. On examination one hour later it was found that these three worker cells were definitely being modified as emergency queen cells and that two more cells containing young worker larvae were being enlarged and flooded with brood food. The experiment was continued for a further hour, making five hours in all, by the end of which time five emergency queen cells had definitely been commenced in nucleus C, but no incipient emergency queen cells could be detected in nuclei A and B.

This experiment was repeated later in the season with another colony of bees, but on this occasion it was six hours before any signs of emergency queen cells could be detected in the control nucleus. Two such cells were found. None were found in either the nucleus containing the queen or in the nucleus which had been fed regularly with bees taken from the nucleus containing the queen.

These results strongly suggest that at least some of the bees that were taken from the queenright nucleus carried with them " queen substance " obtained from their queen and shared it with the bees in the queenless nucleus to which they were introduced, and that the bees in this queenless nucleus obtained sufficient of this substance to inhibit them from producing emergency queen cells.

An attempt to repeat this experiment with a third colony of bees was abandoned as no incipient emergency queen cells could be found in the control nucleus at the end of six hours.[1] As it was felt that further evidence was desirable before the hypothesis that bees are able to inform other members of their colony of the presence of their queen could be accepted, and as the method of experiment just described is not altogether satisfactory, a further type of experiment was designed.

A colony containing about 5000 adult worker bees was divided into two parts, A and B. Each part had combs containing eggs and very young worker larvae suitable for rearing as queens, and the two parts were separated from one another within the same hive-body by a bee-tight screen made of a single thickness of wire-gauze (3 mm. mesh). The bees of the two parts could not join one another. Part A was housed in the front compartment of the hive and its bees could fly in the field. Part B was in the compartment at the back of the hive and its bees were not allowed to fly.

The laying queen of the colony was placed in the outer compartment. In some experiments she was imprisoned in a cage with walls made of queen-excluder zinc ; in others she was imprisoned with a few workers in a cage made of a single thickness of wire-gauze (3 mm. mesh) which reduced the amount of contact her bees in part A could make with her; but, in most cases she was allowed to move about freely amongst her own bees in part A. The bees in part A were always given plenty of pollen and honey, whereas abundant food was provided in part B in some cases but not in others. In those cases in which the bees in part B, the queenless part, were short of food some of the bees in this part clustered on the wire-gauze and solicited and obtained food from the bees in part A. Had they not done so many of them would have died of hunger.

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[1] The speed with which bees will construct emergency queen cells, on being rendered queenless, and the number of cells which they build, varies from colony to colony.

After forty-eight hours both parts were examined for emergency queen cells. The results obtained are shown in Table II.

Table II.—*Effects of method of caging queen and distribution of food on the communication of bees through a wire-gauze screen and upon emergency queen cell production.*

Type of cage in which queen imprisoned in part A.	Distribution of food in parts.		Times used.	Times emergency queen cells built in.	
	A.	B.		A.	B.
No cage used	Plenty	Plenty	6	0	6
Ditto	Plenty	Very little	6	0	2
Perforated zinc cage through walls of which workers could pass	Plenty	Plenty	2	0	2
Ditto	Plenty	Very little	2	0	0
Single-walled wire-gauze	Plenty	Plenty	3	2	3
Ditto	Plenty	Very little	3	3	3
	No queen present in either part.				
	Plenty	Very little	2	2	2

The data presented in Table II indicate that the way in which the queen was caged, and thus the extent to which the bees in part A with her could make contact with her body, determined whether or not emergency queen cells were constructed by these bees. This result agrees with the conclusion reached from examination of the data given in Table I.

In those cases in which the bees in part A (the part in which the free or imprisoned queen was present) built emergency queen cells, the bees in part B also built emergency queen cells, but it did not follow that when the bees in part A built no emergency queen cells none were built in part B. When no emergency queen cells were found in part A and the bees in part B were well fed, emergency queen cells were always found in part B. But when no emergency queen cells were found in part A and the bees in part B were so short of stores that they had to obtain food through the wire-gauze screen from the bees in part A, then in six out of eight cases no emergency queen cells were produced in part B (c.f. Müssbichler, 1952).

When no queen was present in either part emergency queen cells were built in both parts even though the bees in part B were compelled to seek food from those in part A.

It seems reasonable to conclude, therefore, both from these results and those obtained in the two earlier experiments where bees were transferred from queenright to queenless nuclei and no emergency queen cells were built in the latter, that bees that have recently been with their queen and obtained " queen substance " from her are able to " inform " other bees of her presence by giving them a share of the " queen substance " which they have collected. It also seems clear that provided that a group of bees receive sufficient " queen substance " they remain inhibited from building emergency queen cells.

INVESTIGATION OF THE METHODS BY WHICH BEES OBTAIN " QUEEN SUBSTANCE" AND DISTRIBUTE IT AMONGST THE MEMBERS OF THEIR COLONY.

Unfortunately no experimental method of determining the means by which "queen substance " is obtained from the queen and passed around the colony has yet been devised. However, certain observations have yielded data which strongly suggest the method by which this is achieved.

If a laying queen is watched in an observation hive as she moves over the brood combs, it is seen that some of the bees that are nearest to her on the comb pay considerable attention to her. Many of them examine her body with their antennae and others lick it with their tongues. It seems possible, therefore, that these bees are accidentally or, more probably, deliberately collecting " queen substance." In order to obtain some idea of the likelihood of " queen substance " being collected and distributed in one or other of these ways, twelve counts were made at intervals of five minutes of the number of bees which were examining their queen with their antennae and also of the number which were licking her body. The queen was young, mated and laying and headed a colony of about 1500 bees in a small observation hive. The total time spent by individual bees in licking, or examining, their queen on any one occasion was also determined. The results obtained are shown in Tables III*a* and III*b*.

TABLE III*a*.—*Number of bees licking their queen, or examining her with their antennae, at any one time.*

Count number.	Number of bees licking queen.	Number of bees examining queen.
1	3	4
2	3	2
3	4	1
4	2	2
5	3	3
6	4	1
7	4	2
8	0	4
9	1	1
10	0	3
11	3	1
12	3	2
Mean number	2·5	2·2

TABLE III*b*.—*Length of time* (*secs.*) *spent by individual bees in licking or examining their queen on any one occasion.*

	Time spent licking queen (secs.).	Time spent examining queen (secs.).
	58	13
	65	35
	22	16
	22	127
	164	2
	4	6
	30	27
	11	7
	87	50
	198	30
Mean =	66·1	31·3

Observations were next made on the actions of 20 bees in turn which were seen to lick the body of their queen, and 20 bees which examined her with their antennae. Each bee was watched for five consecutive minutes. Every one of the 20 bees seen to lick the queen offered food to at least one other member of her colony within five minutes of leaving the queen, often within a few seconds of doing so, and the majority fed several bees in succession. On the other hand none of the 20 bees seen to examine the queen with their antennae offered food to any other bee within five minutes of leaving the queen, although several of them touched the antennae of other bees with their own. It seems very probable, therefore, that bees obtain the " queen substance " by licking their queen and subsequently transfer some of it to other members of their colony in food which they give to them.

The distance that a bee that has recently been licking her queen will travel in the hive in five minutes is considerable, and the movement that is continually going on would appear to be fully adequate to ensure thorough mixing of the bees of a large colony in a short space of time. In this way it may be assumed that " queen substance " is continually passing round the colony so that the majority of the bees within the hive receive a regular share and are thus inhibited from constructing emergency queen cells.

The part of the queen most frequently licked is her abdomen, and it seems probable that most of the " queen substance " is obtained from this part.

DETERMINATION OF THE PART OF A QUEEN'S BODY FROM WHICH BEES OBTAIN " QUEEN SUBSTANCE."

A small colony containing about 6000 adult worker bees was divided into two approximately equal parts, each part containing adult bees, stores of food and brood of all ages. The two parts were placed in a single brood-chamber and were separated from one another by a bee-tight, vertical, wooden partition. A tightly fitting wire-gauze screen-board over the tops of the frames allowed adequate ventilation and at the same time ensured that the bees in the two parts were completely isolated from, and could not possibly touch, one another. The bees on one side of the wooden partition were free to fly, those on the other side were not.

In the centre of the wooden partition separating the two parts of the colony a hole $1\frac{1}{4}$ in. in diameter was bored. This hole was covered with a tightly stretched sheet of rubber. In the centre of this rubber diaphragm a small hole was made with a red hot needle. The laying queen of the experimental colony was held in the hole in the rubber diaphragm in such a way that her head, or head and thorax and their appendages, were exposed to the bees on one side of the partition, and her thorax and abdomen, or abdomen alone, were exposed to the bees on the other side of the partition. It was found that the bees in the compartment with the head of the queen would continue to feed her for an indefinite period so that in every experiment she remained alive and well. In practice few experiments were continued for more than a week.

Forty-eight hours after a colony had been arranged in this way both parts were thoroughly examined for emergency queen cells. If none were found the experiment was continued for a further forty-eight hours when a further examination was made.

In other experiments the head, head and thorax, or abdomen, of the queen were caged in such a way that the bees could only reach certain limited portions of them or no part of them at all, and in such a way that the bees were either able, or in some cases unable, to obtain any sustance which the queen evacuated from her rectum. The results obtained are shown in Table IV.

TABLE IV.—*The effect on emergency queen cell production of allowing bees access only to certain limited portions of their queen's body.*

Parts of queen's body in compartment A, and their availability to the bees.	Parts of queen's body in compartment B, and their availability to the bees.	Times used.	Times emergency queen cells produced in: A.	B.
Head and thorax—fully available to bees	*Abdomen*—fully available to to bees, together with faeces	7	0	0
Head—fully available to bees	*Thorax and abdomen*—fully available to bees, together with faeces	2	0	0
Head and thorax—fully available to bees	*Abdomen*—protected with wire-gauze cage from bees, but any faeces dropped available to them	5	0	5
Head and thorax—protected with wire-gauze cage from bees (queen fed self from feeder)	*Abdomen*—fully available to bees together with faeces	1	1	0
Head—fully available to bees	*Thorax and abdomen*—protected from bees by polythene tube so that only dorsal surface of thorax available to them	2	0	0
Head—fully available to bees	*Thorax and abdomen*—protected from bees by polythene tube so that only 3 legs and strip of abdomen approx. 2 mm. × 4 mm. available to them	3	0	2

The data obtained in these experiments indicate that it is neither necessary for the bees of a colony to feed their queen nor to collect her faeces in order that they shall obtain "queen substance." Indeed the results shown in Table IV strongly suggest that "queen substance" is obtainable from all parts of a queen's body, but that in order that sufficient "queen substance" may be obtained to inhibit emergency queen cell production by a given proportion of the population of a colony it is essential that these bees should have access to a certain minimum proportion of the body surface of their queen. The smaller the number of bees forming the proportion of their colony, the smaller the minimum area of body surface required.

A working hypothesis was, therefore, formulated in which it was supposed that every laying queen honeybee produces a certain quantity of "queen substance" in a given period of time. If this hypothesis is correct it may be supposed that the bees of any given colony receive a definite quantity of "queen substance" in a given period of time and that if the quantity which they receive is insufficient then the inhibition from emergency queen cell production is removed.

EXPERIMENTS ON THE QUANTITATIVE ESTIMATION OF "QUEEN SUBSTANCE" PRODUCTION.

An experiment was first carried out to determine whether any relationship exists between the number of bees in a colony that has suddenly been deprived of its queen and the number of emergency queen cells built in a given period of time. It was already known that colonies of bees of different strains differ in the number of queen cells which they build, and it was decided to compare the number of emergency queen cells built within 48 hours of the bees being made queenless by colonies of different sizes but of the same strain.

Colonies of two distinct strains, European black and hybrid Carniolan × B.A., were broken down into queenless nuclei of various sizes. Each nucleus was provided with abundant food and larvae of all ages. Forty-eight hours after the experimental queenless nuclei had been made up the number of emergency queen cells present in each was determined. The results obtained are shown in Table V.

TABLE V.—*Relationship between colony size, within a strain, and the number of emergency queen cells produced in 48 hr.* (*Field bees were allowed to return to their parent colonies.*)

	Colony size (approximate number of adult bees).		
	1000–2000	2000–4000	
Number of emergency queen cells built	1	4	Colony A. European black.
Ditto	2	5	,, ,, ,,
,,	1	5	Colony B. European black.
,,	2	5	,, ,, ,,
,,	2	—	,, ,, ,,
Mean	1·60	4·75	
Number of emergency queen cells built	3	9	Colony C. Hybrid Carniolan × B.A.
Ditto	4	23	Ditto
Mean	3·50	16·00	

These data indicate that, within a strain, there is a relationship between the number of adult bees in a queenless colony and the number of emergency queen cells produced within forty-eight hours. The greater the number of bees the greater the number of cells built. (Many more data would be necessary for each strain to determine the exact relationship.) Having decided that such a relationship exists, the following experiment was carried out.

A hollow, brass, cylinder 10 in. long × 6 in. diameter was fitted with bearings which enabled it to be rotated around its long axis which was in a horizontal plane. The cylinder was connected to a small electric motor, through a suitable gear-train, so that when the motor was running it took almost two minutes for the cylinder to complete one revolution. A hole, approximately $1\frac{1}{4}$ in. × $1\frac{1}{4}$ in., was cut in the curved face of the cylinder equidistant from the two ends, and a small wire-gauze cage (3 mm. mesh) was recessed into the cylinder so that its outer wall filled the hole and lay flush with the curved surface of the cylinder.

On either side of the cylinder a hive-body was fitted in such a way that the curved surface of the cylinder formed a part of one of its end walls, and the outer surface of the cage built into the wall of the cylinder became accessible to the bees in each hive body in turn as the cylinder was rotated.

Each hive-body was large enough to hold a maximum of five B.S. deep combs together with about 7000 adult bees.

A contact making and breaking device was fitted to the cylinder to ensure that, when it stopped rotating, the cage, in which a queen was imprisoned, lay inside one or other of the hive-bodies so that the bees in it could feed the queen in the cage and obtain " queen substance " from her body.

A time-clock was designed which switched the current to the electric motor on and off at predetermined intervals of time and thus ensured that the queen was moved, in her cage, out of one hive and into the other. Neither bees nor food were placed in the cage with the queen and the apparatus was so constructed that when the queen was moved automatically from one hive into the other no worker bees were transferred with her.

In a short series of experiments each experimental colony was divided into three nuclei and the field bees allowed to return to their original hives. Each nucleus contained an approximately equal quantity of food and brood in all stages and a known number of adult bees. (A volumetric estimation of the number of bees present was made at the end of each experiment, the bees being anaesthetised.) Two of the three nuclei were placed one on each side of the cylinder; the third, from which the queen was absent throughout the whole of each experiment, which lasted for about 26 hours, was kept as a control. The mechanism was adjusted so that the queen remained in one hive for 6 min. in every hour and in the other hive for 54 min. less the 2 min. taken by the cylinder to revolve. The results of these experiments are shown in fig. 1.

The data shown in fig. 1 support the hypothesis that the bees of a colony that is headed by a mated, laying, queen normally obtain sufficient " queen substance " from her to inhibit them from producing emergency queen cells. If for some reason the bees of a colony do not obtain any " queen substance," as happens when their queen is removed, the inhibition is removed and emergency queen cells are built. Similarly, it is suggested, that if the bees receive an inadequate supply of " queen substance," as in the experiments in which the queen was present for a proportion of each hour, emergency queen cells will be built, the number being proportional to the size of the deficit in "queen substance."

If this hypothesis, or some similar one, is the correct explanation of the facts observed, then one might anticipate that cases may occur in nature in which the quantity of "queen substance" being produced by a laying queen becomes reduced until it is no longer sufficient to "satisfy" her bees and inhibit emergency queen cell production. Queen supersedure,[2] and possibly even the toleration of swarm queen cells by colonies of bees, could be explained in this way. It is probable that "queen substance" is also the factor which normally inhibits the production of "laying workers" in queen-right colonies.

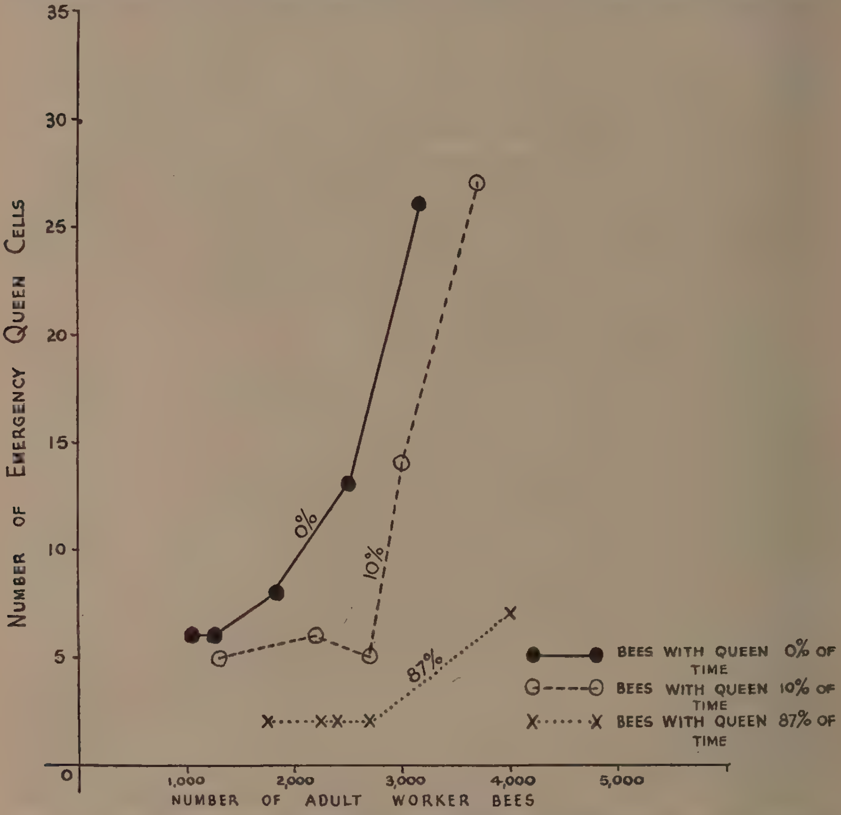

Fig. 1.—Influence of length of time spent by queen per hour with different numbers of bees on number of emergency queen cells built.

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[2] *Queen supersedure.*—Sometimes whilst a laying queen is still present, but appears to be failing in health, her workers will construct a number of emergency queen cells from only one of which a queen will normally be allowed to emerge. After she has mated she will in due course supersede her mother as queen of the colony. It is probable that such supersedure queens sometimes originate from eggs laid by the failing queens in normal queen cells, constructed from the beginning as such by the worker bees.

QUEEN SUPERSEDURE AND THE "QUEEN SUBSTANCE" THEORY.

Normally, provided that they have free access to the body of their mated and laying (or virgin) queen, the bees of a colony will not tolerate the presence of queen cells containing eggs or older stages. However, both when a colony is about to swarm and when it is about to supersede its queen the bees will tolerate, and indeed welcome, such queen cells. If attempted supersedure is due to insufficient production of " queen substance " by the queen, who in such cases is often still present and laying a few eggs, then it should be possible to determine experimentally the number of bees who would continue to be inhibited from emergency queen cell production by the quantity of " queen substance" still being produced by the queen, provided that she is producing any at all.

During the summer of 1953 two colonies of bees (A and B), each of which was fully occupying a B.S. national brood-chamber, were found to be attempting to rear supersedure queens by means of emergency queen cells in the presence of their old laying queens. Each of these old queens were still laying a small number of eggs each day and, apart from their low rate of oviposition, appeared to be perfectly normal. The queen from colony A was taken and placed with about 2000 of her own worker bees on two combs containing food and brood, but no emergency queen cells, in an empty hive. A comb containing eggs and young larvae, but with no adult bees on it, was taken from another colony and given to this small colony. Forty-eight hours later the small colony was examined and it was found that the queen was still present and had laid a few eggs, but that no emergency queen cells had been built. The queen was then taken from the small colony and substituted for the vigorously laying queen of a large colony, her own small colony being left queenless. Forty-eight hours later the now queenless small colony and the large colony were examined. Five emergency queen cells were found in the small, queenless colony and 11 were found in the large colony in which the experimental queen had laid a few eggs. Unfortunately this interesting queen was lost shortly afterwards before she could be used in other experiments.

The queen from the other colony in which emergency supersedure queen cells were found was treated in a similar way. Her colony contained about 20,000 adult workers and had 9 emergency queen cells in various stages of development. She was placed in another hive with about half of her bees (care being taken to see that no emergency queen cells were transferred on the combs with them) and given a comb containing young larvae. The other half of her colony was given a laying queen. Forty-eight hours later it was found that she had laid some eggs but that the bees with her had built 2 emergency queen cells. Approximately half of the bees with her were, therefore, removed together with the emergency queen cells, and another comb containing eggs and young larvae was given. No emergency queen cells were found forty-eight hours later. The experiment was continued for a further forty-eight hours and still no emergency queen cells appeared. Meanwhile no emergency queen cells had appeared in the other half of her colony to which a good laying queen had been given when she was removed. This queen was now removed and the original queen, together with the bees that had remained with her, was substituted. Forty-eight hours later this colony contained 6 emergency queen cells. These cells were broken down and the experiment was continued but when the colony was examined two days later the queen was missing and 8 emergency queen cells had been built.

The results of the experiments with these two queens support the view that queen supersedure occurs when the laying queen of a colony ceases to produce sufficient " queen substance " to " satisfy " the bees of her colony and inhibit them from either building emergency queen cells or tolerating the presence of larvae in queen cells cups.

Low production of " queen substance " appears in each of these cases to have been associated with a low rate of egg production, but it is clear that it is something produced by the queen other than eggs which inhibits emergency queen cell production. If this were not so the bees of the small colonies in which only the heads of the queens were accessible in some experiments (Table IV) would have produced emergency queen cells, which they did not do.

TABLE VI.—*Movements of bees between hives containing various queenless and queenright groups of bees.*

Condition of groups of bees at start of experiment.		Number of times experiment carried out.	Condition at end of experiment, number of times all bees found in :	
Hive A.	Hive B.		Hive A.	Hive B.
Bees from colony with mated laying queen, *queen not present*	Bees from colony with mated laying queen, *queen not present*	6	No obvious movement of bees between hives in 2 experiments 1	3
Bees from colony with mated laying queen, *queen not present*	Bees from colony with mated laying queen, *queen present*	6	0	6
Bees from colony with mated laying queen, *queen present*	Bees from colony with mated laying queen, *queen present*	6	0 (groups remained discrete)	0
Bees from colony with mated laying queen, *queen present*	Bees from colony with virgin queen, *virgin present*	6	Groups remained discrete in all experiments	
Bees from colony with mated laying queen, *queen present*	Bees from colony with virgin queen, *virgin absent*	6	6	0
Bees from colony with mated laying queen, *queen absent*	Bees from colony with virgin queen, *virgin present*	6	0 (on 2 occasions the virgin queen was " balled ")	6
Bees from colony with virgin queen, *virgin present*	Bees from colony with virgin queen, *virgin present*	6	Groups remained discrete	
Bees from colony with virgin queen, *virgin present*	Bees from colony with virgin queen, *virgin absent*	6	6	0

Experiments to Determine whether Worker Bees which have Lost their Queen will enter the Hive of a Strange Colony in Search of "Queen Substance."

Two small hives (A and B) were arranged with their entrances communicating with a small, covered, arena 9 in. × 9 in. × 1 in. deep. The bees placed in these hives could not fly but were free to move in an out of the arena, and it was possible for the bees in either of the hives to move across the arena and join the bees in the other hive. Each hive was filled with combs containing honey and pollen but no brood. A group of about 1500 worker bees, with or without a queen, was placed in each hive at about 5 p.m. in the evening, and at 9 a.m. the next morning any mass movements of the bees from one hive to the other which had taken place during the night were recorded. The results are shown in Table VI.

It is clear from the results shown in Table VI that whereas there was some tendency for queenless groups of bees to join together to form a single group, no such tendency was shown when each group possessed a queen. This was true irrespective of whether the two queens were both mated, laying, queens, or both virgins, or one a mated laying queen and the other a virgin. On the other hand in all experiments in which a mated, laying queen was present in one hive and no queen present in the other, the queenless group of bees moved across the arena and joined the bees with the laying queen. It made no difference to the result whether the queenless group of bees was taken from a colony possessing a mated, laying, queen or from one with a virgin queen. Similarly if one hive contained a virgin queen and the other had no queen, the queenless group of bees, whether taken from a colony headed by another virgin queen, or from one with a mated, laying queen, always joined the queenright group of bees. But it will be noted that in two cases where the queenless group of bees had been taken from a colony headed by a mated laying queen immediately before the experiment, the virgin queen in the queenright group was " balled ",[3] the bees forming the ball around her attempting to kill her. It could not be determined which group of bees " balled " the virgin but it seems probable that it was bees from the colony with a laying queen which did so. It appears, therefore, that any group of queenless, broodless, worker bees has a very strong urge to join any queenright colony of which its members become aware. The bees do this, presumably, on account of the presence of the queen, whether she is a virgin or a mated queen, as they show no urge to join another group of bees if they have a queen of their own and no pronounced urge to join another group of queenless bees. This strongly suggests that they do so for the sake of something which they can obtain either directly from the queen herself or from the bees that are with her. It is suggested that what they seek is " queen substance."

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[3] The term " balling " is used in the present paper to describe the clustering together on top of and around a strange queen, of an aggressive group of worker bees some of whom are holding on to her limbs with their mandibles, whilst others are attempting to sting her to death. Worker bees which attempt to enter the hive of a strange colony, although often mauled by the guard bees, are not " balled " in this way (see Butler and Free, 1952). However, worker bees belonging to a colony headed by a mated, laying, queen, which have been " balling " a virgin queen which has been introduced into their hive sometimes become contaminated with some substance (virgin " queen substance ") from the body of the virgin queen and are subsequently " balled " by members of their own colony (Butler, 1952).

Observation has shown that a large number of bees from each hive met one another in the arena and that in many cases food was interchanged between the bees of each group. There was, however, a much greater tendency for the bees belonging to a group with a laying queen to offer it to other bees than there was for bees of a queenless group to do so. (In one experiment the bees belonging to the groups were of distinctive colours, and in 59 cases of food interchange observed, bees from the group which had a mated, laying, queen gave the food to bees from the other group which was queenless in 18 cases, and to members of their own group in 26 cases; only in 6 cases was a bee from the queenless group seen to feed a bee from the laying-queen group, and in 9 cases to feed a bee of her own group.) As earlier observations, already discussed, have shown that bees that have just licked their queen have a strong urge to offer food to other bees there is good reason to suppose that the bees from the queenright groups in the arena which offered food to bees from queenless groups were actually offering them food containing " queen substance " and that in this way the bees of the queenless group learned of the presence of the queen in the hive of the queenright group and, ignoring the different odour of the bees of this group—an odour difference of which they were undoubtedly aware (Butler and Free, 1952)—gradually infiltrated into the hive containing the queen. The urge to obtain " queen substance " appears to have overcome their inherent tendency only to consort with bees with the same colony odour as their own.

Discussion.

It is concluded that queen honeybees produce a substance (present on all parts of the body surface) which is extremely attractive to worker honeybees. Some of the workers of a colony who are nearest to the queen at any given time obtain supplies of this substance by licking the queen's body, particularly her abdomen. These bees quickly and widely share this " queen substance " with other members of their colony. In this way the workers are made aware of the continued presence of their queen in the colony.

Park (1923) and Nixon and Ribbands (1952) have produced evidence of widespread food sharing amongst the adult worker honeybees of a colony, and Ribbands (1952) has suggested that such food sharing forms the basis of social life in honeybees.

It may very well be true that the most important substance which is shared amongst the members of a colony is this " queen substance."

How powerful this appetite for " queen substance " can become is shown by the fact that although normally antagonistic towards workers with body odours differing from their own (Butler and Free, 1952), groups of queenless worker bees belonging to different colonies, and possessing different body odours from those of other groups with queens, under certain experimental conditions will invade the hives of the latter in search of " queen substance."

Castle (1934) and Light (1944), amongst others, have described how groups of worker termites constantly seek some substance from the bodies of their queens by licking them. It has also been shown that worker army ants seek some substance from their queen (Schneirla, 1953). It seems possible, therefore, that in all the groups of social insects, except perhaps the wasps, " queen substance" serves as a most important factor in the maintenance of colony cohesion.

This view is clearly similar to that of Wheeler (1928) that reciprocal feeding is the " social medium " of termites, ants and wasps, and possibly of all other social insects.

In the case of honeybees, termites (Emerson, 1939) and the army ant (Schneirla, 1953) this " queen substance " received by the workers constitutes a chemical co-ordinating agent which serves to inhibit the production of additional queens. Provided that the worker honeybees of a colony obtain sufficient " queen substance " they are inhibited from building emergency queen cells and also, probably, from constructing swarm queen cells. Should the supply of " queen substance " become reduced the worker honeybees will (if they possess suitable female larvae) construct emergency queen cells, the number built by bees of any one strain being greater the larger the deficiency of " queen substance." Absence of " queen substance " also probably results in removal of the factor which inhibits the development of " laying workers " under conditions in which they would otherwise appear.

Both in the case of the honeybee and in the case of the army ant (Schneirla, 1953) queen supersedure appears to be brought about by a reduction below a definite threshold of the quantity of " queen substance " available to the workers. In neither case does supersedure appear to be directly connected with a reduction in the reproductive capacity of the queen but rather to some organic change which is accompanied by a reduction in the queen's stimulative attractiveness and inhibitory efficiency to workers. A reduction in the quantity of " queen substance " may be considered to be associated with such organic degeneration.

" Queen substance " is necessarily somewhat fugitive. Bees given an opportunity to lick the body of their newly dead queen only continue to do so for an hour or two and then show no further interest in her, and the amount of " queen substance " which they obtain is only sufficient to postpone emergency queen cell production for a very short time.

Filter paper which has been rubbed on the body of a queen loses its ability to arouse the interest of bees after being exposed to the air for a short time. This is also true in the case of termites (alcoholic extract, Emerson, 1939) and of the army ant (filter paper absorption, Schneirla, 1953).

Nothing definite is known about the nature of the " queen substance " in the honeybee. It appears possible, however, that it may be part of the waxy substance with which the body is covered or, more probably, of the volatile solvent in which the waxes are believed to be secreted (Beament, 1951). It seems reasonable to suppose that the wax solvent of the queen honeybee contains some substance not found in the wax solvent of the worker, but of great attraction to the latter.

In the case of the honeybee there is no doubt that, although both virgin and mated, laying, queens are attractive to workers, the latter are able to distinguish between the two very quickly. The workers of a colony headed by a mated, laying, queen will usually attempt to kill any virgin queen who enters their hive. Workers of the army ant can similarly distinguish between virgin and old, laying, queens. (Schneirla, 1953). The nature of this distinction is being investigated by the author in the case of the honeybee, and it appears likely that there is some difference in the quality of the "queen substance" produced by virgin and mated, laying, queens respectively. On the other hand, virgin queens all appear to produce a "queen substance" of similar quality, as do mated, laying, queens.

SUMMARY.

1. The method by which worker honeybees recognise the presence of their queen has been investigated.

2. A definite sign that a colony has realised its queenlessness is emergency queen cell construction.

3. Mated, laying, queens were caged in various ways which restricted the extent to which their workers had access to them. It was found that unless the bees had fairly easy access to their queens they built emergency queen cells. The larger the colony the more accessible must be the queen. This suggests that bees normally obtain some substance from their queen which inhibits them from building emergency queen cells provided that a sufficient quantity is obtainable.

4. It is most unlikely that every member of a colony obtains her share of "queen substance" directly from the queen, and experiments in which groups of worker bees could only obtain "queen substance" from other workers showed that this is the case.

5. Observation has shown that a small proportion of the bees of a colony obtain "queen substance" by licking the body, particularly the abdomen, of their queen and then offer food to other members of their colony. It is believed that in this food "queen substance" is widely shared amongst the members of a colony.

6. Experiments have shown that worker bees can obtain "queen substance" from all parts of the bodies of their queens; furthermore, that the smaller the number of bees in a group, the smaller the area of their queen's body surface to which they must have access in order to remain inhibited from producing emergency queen cells.

7. The number of emergency queen cells built in forty-eight hours by a group of bees of any one strain is dependent upon the number of bees forming the group.

An apparatus was devised which allowed access of separate groups of bees from the same colony to their queen for predetermined periods in every hour, to confirm that a certain minimum quantity of "queen substance" per unit time is necessary to inhibit a given number of bees from building emergency queen cells.

8. In nature emergency queen cells are sometimes found in colonies whose bees are attempting to supersede failing queens. During 1953, experiment showed in two such colonies that although the queen was producing sufficient "queen substance" to inhibit a small number of her workers from building emergency queen cells, she was not producing enough to inhibit their production by her colony as a whole.

9. Data were obtained which indicate that worker honeybees actively seek "queen substance." An adequate supply of this substance, besides inhibiting the production of queen cells, also probably inhibits the development of "laying workers."

10. Worker termites and worker army ants also obtain some substance from their queens by licking them, and this inhibits the production of further queens provided that the workers obtain sufficient of it.

It therefore seems highly probable that in all the groups of social insects, except perhaps the wasps, the collection and distribution of "queen substance" is the most important single factor in the maintenance of colony cohesion.

11. It is further suggested that the " queen substance " may be a part of the waxy covering of the queen's body, or, more probably, of the volatile solvent in which the wax is believed to be secreted.

12. Both worker honeybees and army ants can readily distinguish between virgin and old, mated, queens. The nature of this distinction is being investigated in the case of the honeybee and appears to be due to some difference in the quality of the " queen substance " produced by the two types of queens.

ACKNOWLEDGMENTS.

I wish to express my gratitude to all those who have helped me with suggestions and criticisms during the course of this work. My thanks are especially due to Messrs. L. Bailey, J. Simpson and R. Welch.

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Vol. 105. Part 3. Pp. 31–63. 16 figs. 11th May, 1954

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STUDIES ON THE LIFE HISTORY AND ECOLOGY OF *DILTA LITTORALIS* (WOMERSLEY, 1930) (THYSANURA, MACHILIDAE).

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Manuscript received 14th July, 1953.
(Read 4th November, 1953.)

With 16 Text-figures.

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I. INTRODUCTION.

STUDIES of the Thysanura, outside the fields of taxonomy and morphology, are remarkably few, the more noteworthy contributions to the biology of the Order having been provided by Willem (1924), Sweetman (1938) and Wygodzinsky (1941). The British contributions since Lubbock's monograph (1873) have been entirely in the form of short taxonomic papers which Delany (1953*a*) has incorporated in a recent revision of the British representatives of the Order.

Accounts of the systematics, morphology, and post-embryonic development of the genus *Dilta* have been given by Verhoeff (1910*a*, 1910*b*), Bär (1912) and Wygodzinsky (1941), whilst a study of the biology and geographical races of *D. hibernica* Carpenter has been provided by Kratochvil (1945). In addition to his systematic study Wygodzinsky (1941) made a brief survey of the ecology and biology of this and allied genera occurring in Switzerland.

Dilta littoralis Womersley is one of the three indigenous British species of a genus of nine known species restricted in their distribution to the continent of Europe and its surrounding islands. It was first described by Womersley (1930) and its nomenclature corrected by Argilas (1939) who, in a subsequent paper (1941), described its spermatogenesis and certain aspects of its morphology.

The approach employed in the present autecological study has been to determine how, in limited areas of heathland, the life history and distribution of *D. littoralis* integrates in time with its associated animal and plant communities. A broad outline of the features of this habitat has been given by Pearsall (1950) and contributions to its invertebrate fauna by Richards (1926) and Cheetham (1942, 1943). The only other work undertaken in this locality has been by Harvey (1938) on grasshopper distribution.

ACKNOWLEDGMENTS.

The author wishes to express his gratitude to Professor L. A. Harvey for his most helpful supervision throughout the course of this research. He also wishes to acknowledge the considerable assistance rendered by Mr. W. D. Hincks, Mr. T. H. Savory, and Dr. A. F. Millidge and Mr. J. G. Blower in their identification of the Coleoptera, Araneida and Myriapoda respectively.

The work was undertaken whilst in receipt of a Nature Conservancy Research Studentship.

II. LIFE HISTORY.

1. Technique.

It was apparent from the outset of the ecological study that methods had to be devised that would, as time progressed, throw light on breeding habits, longevity, sex size and ratio and growth rate of *Dilta littoralis*. Certain habitats were being investigated on a round-the-year basis and from these there would come indications of breeding by increase in their populations. Although an aid to the study of the life history, this in itself was felt to be inadequate and in order to supplement it the body length, and whenever possible the sex was determined of every animal captured. Watkins (1941) was able to obtain good results on the life history of the Amphipod *Corophium volutator* Pallas by measuring the body length of his animals at different times of the year. He had the advantage of being able to obtain very large numbers. Harker (1952) also used this method in her study of the life histories of four species of may-flies.

Measurement of animal length was facilitated by placing a living animal in a petri-dish beneath which was a scale graduated in mm. The animal was then observed through a low-power binocular microscope and the body length read off directly. This method required a certain amount of patience as the observer had to wait until the animal remained motionless with its body perfectly straight. Living animals were measured in every instance. By this method sizes can be measured to the nearest 0·5 mm. The measurement taken was from the most anterior region, but excluding such appendages as the maxillary palps, to the base of the median caudal furca. The reason for not including the median caudal furca is that the latter is frequently absent or shortened in insects collected in the field.

To sex the insects one was gently held, with the ventral surface uppermost, between the thumb and forefinger of the left hand and the posterior ventral plates covering the external genitalia opened with a small needle, held in the right hand. It was not found practicable to carry out this process on animals less than 7 mm. long because the external genitalia are not easily recognisable until this length is attained. The examination was undertaken under a low-power binocular microscope. It was only the occasional animal that was at all damaged by this method of examination.

Whenever collections were made every individual was taken in order to avoid any form of sampling bias.

2. Results.

Insect length was measured over the period January, 1951 to July, 1952, and the results are displayed in Table I.

The figures are expressed, in the main, by the month. However, in view of the scarcity of insects from March to June, 1951, the lists represent two-month periods and a half-month period in July when numbers were high and growth rapid. The figures for eight representative periods have been displayed graphically in figs. 1–8.

The first very young forms (fig. 3) were collected in 1951 on 4th July and their absence prior to this date suggests a hatching in late June and early July. That it does not occur on a large scale later than this is shown by the low proportion of very small specimens taken in the latter half of the month (fig. 4). The appearance of a newly hatched individual on 23rd May, 1952, and, although no census was made, the observation of a number in June suggests a rather earlier hatching in that year. The size increase of the generation hatching in 1951 can be followed through August (fig. 5), November (fig. 6), January (fig. 7) and May (fig. 8) where by virtue of its smaller size it remains distinct from that of the previous year. The January, 1951 (fig. 1) distribution with its peak at 7·5 mm. is equivalent to that with a peak of 7 mm. in the January 1952 sample and therefore represents the hatching of the previous June. On tracing this generation forwards it can be seen (Table I) to represent the smaller of the two

TABLE I.—*Grouping of* Dilta littoralis (*Wom.*) *in sizes and sexes per period time.* (*J = unsexed juveniles.*)

Body length (mm.).	1951.																							
	January.			February.			Mar./Apr.			May/Jun.			July 1–14.			July 15–31.			August.			September.		
	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
2·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	2	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	21	.	.	.	.	.	.
3·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	26	.	.	.	.	.	.
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	25	.	.	1	.	.	.
4·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	4	.	.	2
5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.	.	4
5·5	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	49	.	.	19
6	.	.	1	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	37	.	.	17
6·5	.	.	9	.	.	5	.	.	7	.	.	4	.	.	.	.	.	.	.	.	17	.	.	19
7	6	12	.	4	6	.	3	2	.	2	1	.	.	.	.	.	.	.	.	.	.	10	11	.
7·5	18	23	.	7	4	.	1	3	.	7	10	.	2	.	.	.	1	.	.	.	.	3	4	.
8	10	8	.	.	3	.	1	5	.	3	3	.	5	4	.	2	.	.	1	.	.	.	.	.
8·5	7	3	.	.	.	.	.	.	.	.	1	.	5	4	.	4	.	.	.	.	.	.	.	.
9	1	2	.	.	.	.	1	.	.	.	.	.	.	1	.	4	10	.	3	.	.	1	.	.
9·5	3	1	.	.	3	.	.	1	.	.	.	.	.	3	.	.	8	.	1	1	.	4	2	.
10	4	2	.	.	1	.	.	1	.	.	.	.	.	1	.	.	.	.	1	5	.	7	5	.
10·5	.	2	.	.	2	.	.	1	.	.	1	.	.	.	.	.	.	.	.	10	.	1	6	.
11	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	1	.	.
Total	49	54	11	11	19	6	6	13	9	12	16	4	12	13	21	10	19	82	6	20	126	27	28	61

Body length (mm.).	1951.									1952.											
	October.			November.			December.			January.			February.			May.			July 1–14.		
	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.	♂.	♀.	j.
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
2·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
3·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
4·5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
5·5	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.
6	.	.	3	.	.	9	.	.	4	.	.	3	.	.	16	.	.	5	.	.	.
6·5	.	.	16	.	.	20	.	.	14	.	.	17	.	.	19	.	.	26	.	.	.
7	20	15	.	10	19	.	15	11	.	13	20	.	7	6	.	27	33	.	.	.	.
7·5	7	13	.	10	12	. .	8	10	.	3	12	.	1	.	.	27	58	.	1	.	.
8	.	3	.	3	4	.	4	2	.	4	.	.	.	.	.	5	14	.	5	.	.
8·5	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	3	4	.	7	1	.
9	2	1	.	1	.	.	3	.	.	.	.	.	1	1	.	.	4	.	1	1	.
9·5	4	3	.	4	1	.	8	.	.	5	.	.	4	1	.	1	2	.	.	2	.
10	1	3	.	8	12	.	8	6	.	1	3	.	1	11	.	.	1	.	.	2	.
10·5	.	4	.	.	6	.	4	12	.	2	6	.	1	3	.	.	1	.	.	2	.
11	.	.	.	.	3	.	.	2	.	.	4	.	.	2	.	.	.	.	.	.	.
Total	34	42	21	36	57	29	51	45	18	28	45	21	15	24	37	63	117	32	14	8	24

groups until July when, with the appearance of the new generation, it assumes adult status and finally disappears between May and July of the following year. During May and June of 1951 and 1952 the elder generation has represented thirteen of the two hundred and sixty-four (approximately 5 per cent.) individuals collected. Thus, as two (never more or less) generations have been collected at all times of the year it appears probable that the maximum longevity of an individual is approximately two years.

The statistical analysis of the data (Table II) has involved the calculation of means (m), standard deviations $\left(\sigma = \Sigma\sqrt{\frac{(d)^2}{N}}\right)$, standard errors of means and standard deviations and the variance (σ^2) of the younger (subsequently referred to as juvenile) and adult male and female generations. At periods when the body lengths of the populations of two generations have overlapped, the size group, between the two peaks, with the smallest number of representatives has been taken as the midpoint between them and its members divided equally between the two populations. In the case of an uneven number of individuals in any particular group, the odd one has been attributed to the larger population.

From it there appears a substantial difference in the mean lengths of the adult males and females and in consequence the data have been analysed further. Adults of January, 1951, July, 1951 to February, 1952, and July 1952, have

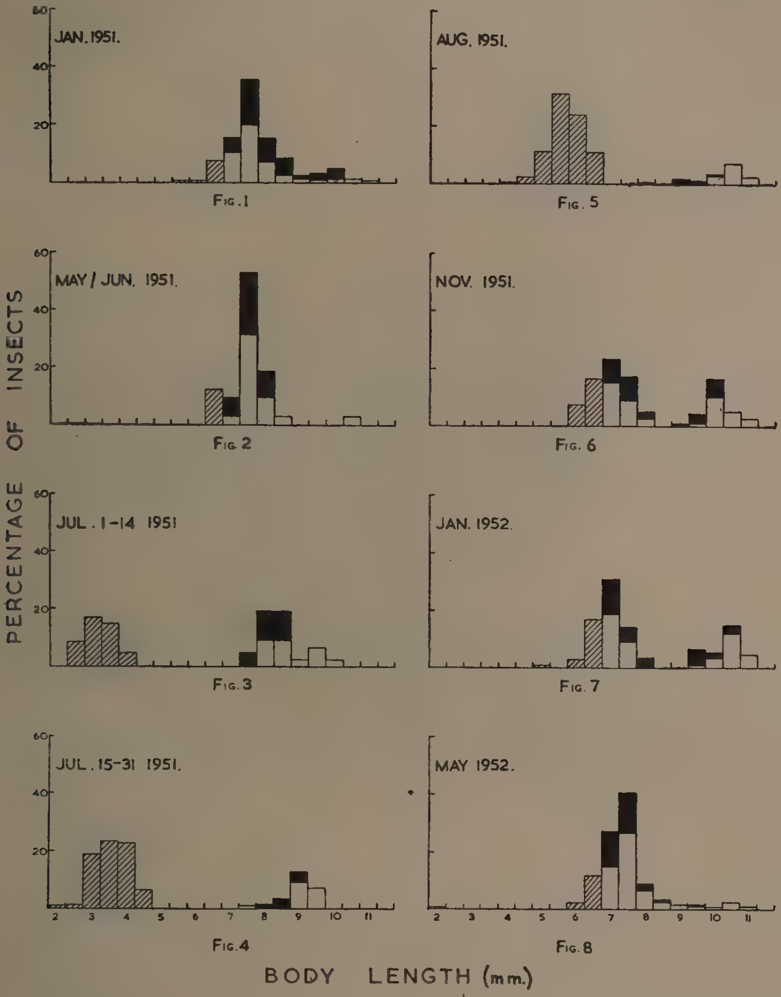

Fig. 1 Fig. 5

Fig. 2 Fig. 6

Fig. 3 Fig. 7

Fig. 4 Fig. 8

Figs. 1–8.—Histograms, obtained from collections made in the stated periods, displaying the relative abundance of juveniles and sexed adults of *Dilta littoralis* (Wom.) according to their body lengths. The juveniles are represented by cross-hatching and the adult males and females by black and white respectively.

TABLE II.—*The mean body lengths (mm.), the standard deviations and their standard errors, and the variance of the juvenile (M_j, σ_j and σ_j^2), adult male ($M_♂$, $\sigma_♂$ and $\sigma_♂^2$) and female ($M_♀$, $\sigma_♀$ and $\sigma_♀^2$) generations of* Dilta littoralis *(Wom.) for the periods stated.*

	1951.			
	January.	February.	March/April.	May/June.
M_j	7·505±0·0608	7·169±1·3490	6·961±0·0847	7·452±0·1050
σ_j	0·6082±0·0430	0·7390±0·0954	0·5222±0·0599	0·4812±0·0742
σ_j^2	0·3799	0·5401	0·2728	0·2315
$M_♂$	9·786±0·0234	.	9·0000	.
$\sigma_♂$	0·0612±0·0164	.	.	.
$\sigma_♂^2$	0·0037	.	.	.
$M_♀$	10·071±0·1465	9·743±0·0241	10·000±0·0962	10·500
$\sigma_♀$	0·3877±0·1036	0·0590±0·0016	0·1667±0·0680	.
$\sigma_♀^2$	0·1503	0·0035	0·0278	.

	1951.			
	July 1–14.	July 15–31.	August.	September.
M_j	3·167±0·1046	3·567±0·0601	5·667±0·0464	6·319±0·0862
σ_j	0·4796±0·0740	0·5439±0·0427	0·5210±0·0329	0·8355±0·0606
σ_j^2	0·2320	0·2958	0·2714	0·6981
$M_♂$	8·125±0·0535	8·600±0·0557	9·083±0·1501	9·808±0·0377
$\sigma_♂$	0·1857±0·0379	0·1760±0·0393	0·3678±0·1061	0·1360±0·0267
$\sigma_♂^2$	0·0345	0·0310	0·1353	0·0185
$M_♀$	8·731±0·0124	9·132±0·0621	10·432±0·0308	10·214±0·0645
$\sigma_♀$	0·4467±0·0911	0·2707±0·0439	0·1445±0·0223	0·1684±0·0318
$\sigma_♀^2$	0·0911	0·7327	0·0210	0·0284

	1951.			1952.
	October.	November.	December.	January.
M_j	6·998±0·0684	6·983±0·0594	7·170±0·0763	6·937±0·0598
σ_j	0·6076±0·0496	0·5512±0·0420	0·6520±0·0540	0·5107±0·0423
σ_j^2	0·3693	0·3038	0·4251	0·2608
$M_♂$	9·429±0·0387	9·786±0·0276	9·857±0·0371	9·864±0·0464
$\sigma_♂$	0·1024±0·0274	0·0994±0·0195	0·1699±0·0276	0·1540±0·0328
$\sigma_♂^2$	0·0105	0·0098	0·0289	0·0237
$M_♀$	9·955±0·0747	10·250±0·0328	10·400±0·0201	10·434±0·0297
$\sigma_♀$	0·2479±0·0529	0·1534±0·0231	0·0900±0·0160	0·1423±0·0210
$\sigma_♀^2$	0·0615	0·0187	0·0081	0·0202

	1952.		
	February.	May.	July 1–14.
M_j	6·343±0·0642	7·295±0·0376	3·208±0·1065
σ_j	0·4585±0·0454	0·5560±0·0266	0·5219±0·0753
σ_j^2	0·2101	0·3136	0·2724
$M_♂$	9·643±0·0733	9·5000	8·143±0·0409
$\sigma_♂$	0·1940±0·0518	.	0·1531±0·0289
$\sigma_♂^2$	0·0376	.	0·0234
$M_♀$	10·111±0·0495	10·227±0·1071	9·688±0·1565
$\sigma_♀$	0·2099±0·0350	0·3553±0·0758	0·4427±0·1107
$\sigma_♀^2$	0·0441	0·1262	0·1960

been selected as they have been present in larger numbers. The comparisons have been made in all cases for means of two small samples (Snedecor, 1946) where

$$t = \frac{m_{♂} - m_{♀}}{\sqrt{\sigma^2_{♂+♀}\,(n_{♂} + n_{♀})/n_{♂}\,n_{♀}}}$$

and $m_{♂}$ and $n_{♂}$ are respectively the mean and frequency of the males and $m_{♀}$ and $n_{♀}$ are the same for the females, with $\sigma^2_{♀+♂}$ the pooled variance of both males and females. The statistical figures are :

		$m_{♂} - m_{♀}$	*t*.	Degrees of freedom.	*P*.
1951 . . .	Jan.	0·2619	1·0401	12	$>0{\cdot}3$
	July 1–14	0·3494	2·5530	23	$<0{\cdot}02$
	July 15–31	0·7556	2·3130	27	$<0{\cdot}05$
	Aug.	0·2071	3·9152	26	$<0{\cdot}001$
	Sept.	0·1651	2·5942	25	$<0{\cdot}02$
	Oct.	0·2151	2·3482	16	$<0{\cdot}05$
	Nov.	0·1414	3·6520	33	$<0{\cdot}001$
	Dec.	0·1377	4·6810	39	$<0{\cdot}001$
1952 . . .	Jan.	0·1552	2·1654	32	$<0{\cdot}05$
	Feb.	0·2233	2·2180	23	$<0{\cdot}05$
	July 1–14	0·2842	6·9910	20	$<0{\cdot}001$

Since *P* is greater than 0·05 only once, and even then on the basis of the smallest sample, a significant sex size difference of adults of all ages is indicated. By using Arithmetic Probability Paper (Harding, 1949) in an analysis of the juvenile populations for May and June, 1951 and 1952, it has been possible to determine whether this difference occurs prior to the animals becoming adult. The juvenile samples did, in fact, conform to a unimodal distribution. The majority of these body lengths were obtained in May and, as a significant sex-size difference appears in the same generation in the following July, the differential growth rates must be proceeding by June.

By graphing the mean lengths of the juveniles and adult males and females against time (fig. 9), the rate and period of growth are displayed. Growth is at a maximum from May to September and is far greater in the juveniles during this period than in the adults. It is virtually at a standstill for the rest of the year. A slight difference in the longevity of the two sexes is indicated by the small percentage of adult males collected between March and June, when only two of the sixteen adults were males.

On the basis of the above data the maximum longevity of *D. littoralis* in south-west England approximates to two years, this being similar to that of *D. hibernica* f. *virgo* Kratochvil in Moravia (Kratochvil, 1945). Argilas (1941) found *D. littoralis* in the vicinity of Bordeaux to have representatives of three distinct size groups concurrently during the summer months which suggests a rather longer length of life in that district. In his observations on *Dilta* sp. in Switzerland, Wygodzinsky (1941) claimed it to have a longevity of 2–3 years and to display a growth of 2 mm. during the winter months ; these phenomena have not been observed in this study. Both the latter authors supported their statements with little factual evidence. Wygodzinsky (1941) has drawn attention to the variation in longevity with geographical location in certain species of *Machilis* and such a possibility cannot be discarded in respect to

Dilta. None of these authors have been able to determine the time of egg-laying or mating in this species although Argilas (1941) was able to describe spermatogenesis only from males collected in late summer, and only during this period did he observe females to be gravid. Eggs have never been laid in the laboratory or collected in the field but the author has dissected females throughout the year and only found them gravid in July. The mean number of eggs observed within six such females was 15 ± 2·08; a figure intermediate between the 2–8 laid by *Trigoniophthalmus* Verhoeff and the 14–32 of fully adult *Machilis* (Wygodzinsky, 1941). This suggests the period of egg-laying to be during August very soon after mating, with the commencement of hatching late the following spring. In the allied species, *D. hibernica*, Kratochvil (1945) observed egg-laying in July and August. The overwintering of eggs is not an uncommon feature of the Machilidae, Wygodzinsky (1941) having noted its occurrence in *Machilis* and *Trigoniophthalmus* as has the author in *Petrobius* Leach. The exact time of hatching is probably variable; Bär (1912) collected very young forms of *Dilta* in May, Kratochvil (1945) in July and in this study they have been obtained in May, June and July.

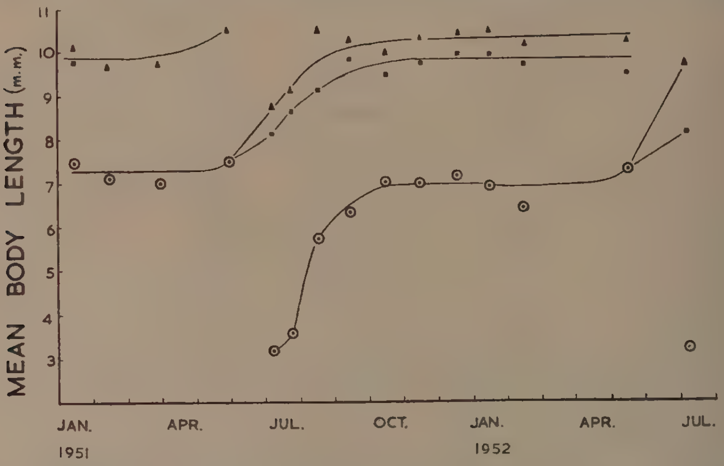

Fig. 9.—Graphs illustrating the mean body lengths, in most cases by the month, of portions of the generations of *D. littoralis* hatching between 1949 and 1952. The juveniles and adult males and females are represented by circles, squares and triangles respectively.

The ratio of males to females for portions of three generations has been calculated for the periods shown:

		Hatched.		
		1949.	1950.	1951.
1951	Jan.–June	0·1	0·833	.
	July–Sept.	.	0·526	0·889
	Oct.–Dec.	.	0·774	0·930
1952	Jan.–June	.	0·365	0·632
	July 1–14	.	.	1·750

In the generation born in 1951, as far as sexing was possible, the figures indicate a slightly higher number of females than males. At the other end of their life the January to June figures of the disappearing generations in 1951 and 1952 display a marked minority of males and thereby lend support to the view that the males have a shorter life than the females. The intervening period is one of fluctuation in relative numbers but only in July, 1952, when only a small sample was available, have males been found to be more abundant than females. Verhoeff (1910*b*) discussed the possibility of *Dilta* being parthenogenetic but, whilst the females are in the majority, the males are never at such a relatively low density to make this probable.

III. THE ECOLOGICAL SIGNIFICANCE OF THE LIFE CYCLES OF CERTAIN MACHILIDAE.

The type of life-cycle displayed by *D. littoralis* is of considerable ecological significance especially with reference to population studies. That it takes two years to complete and that each generation only breeds once, and then over a limited period, exhibits the coexistence of two genetically isolated populations. This is spoken of by Allee *et al.* (1949) as annual cyclic isolation and is observed to be of rare occurrence. It follows that of the two generations collected at any one time there exists no direct interdependence of their densities as the parents of the younger individuals are of the generation whose last survivors disappeared in the June of their hatching, and are not those individuals found with them. In a study of such short duration as this it has not been possible to assess the extent of density differences in the two populations. From Kratochvil's (1945) account of the life cycle of *D. hibernica* f. *virgo* similar conditions are to be found in Moravia but in the Gironde a gene flow between the populations of *D. littoralis* (Argilas, 1941) may be possible, the individuals in that locality having an increased longevity, and in consequence a second breeding period may occur. This would permit mating between members of different generations.

In view of this anomalous life-cycle those of three other Machilid genera have been considered and are schematised in fig. 10. In *Machilis* and *Lepismachilis* Verhoeff cyclic isolation is improbable, only occurring if mating between members of different generations is not possible. In contrast it appears probable in *Trigoniophthalmus*, and if Wygodzinsky's (1941) estimates of its longevity are correct, three isolated populations must coexist in high mountain habitats.

This cyclic isolation of populations of the same species is genetically unusual and it is tentatively suggested, but with little factual evidence that it may be overcome by one or both of two methods. Firstly, a very small percentage of females may survive to a second breeding season. This would involve mating with a male of the succeeding generation and ultimately the production of a generation of mixed composition. Secondly, and more improbably, a number of eggs may hatch the second spring after laying instead of the following as anticipated. Should either or both of these phenomena occur, it appears improbable, in view of the evidence available, that they would be on sufficient scale greatly to influence the apparent lack of direct population density relationships between the coexistent generations.

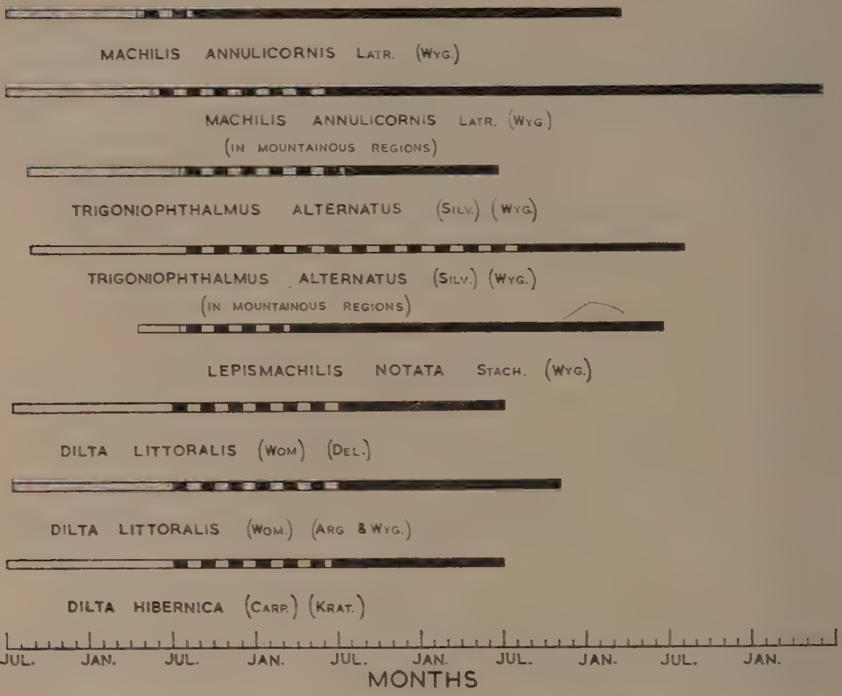

Fig. 10.—A diagrammatic representation of the life histories of various species of Machilidae. The source of each is cited in the brackets following the specific authority. The period each species spends as an egg, juvenile and adult are shown respectively by the white, broken black and white and solid black blocks.

IV. Distribution.

The distribution of *Dilta littoralis* has been considered as its occurrence in its widest sense, embracing its appearance at the biogeographical and much more local environmental levels, and in consequence it has been found convenient to consider it from three aspects :

1. Geographical
2. Plant community relationships.
3. Intra plant community relationships.

Geographical studies aim to describe occurrence on a national or sub-national scale and it is at this level that presence or absence within the British Counties and Vice-Counties is considered. Their importance lies in providing a guide to the major geographic and climatic barriers limiting distribution.

Plant community work aims at assessing the presence or absence of *Dilta* within a plant community, e.g., woodland, heathland. And finally at the intra-community level the problem is examined of how, in numbers, arrangement and time, the species distributes itself in the plant communities it inhabits.

Clark (1948) stressed the value of such studies in grasshopper ecology, many of his statements being equally applicable to the Thysanura which, like the Acrididae he dealt with, are relatively stationary. This basic knowledge of the distribution of a species subsequently contributes much towards a complete understanding of its ecology.

Owing to the absence of information, a consideration of the early history of its distribution has not been possible. It is therefore beyond the scope of this paper to consider to what extent the present distribution has been governed by earlier physical and biological influences.

1. Geographical Distribution.

The recorded geographical range of *D. littoralis* lies within the maritime region of Western Europe and extends discontinuously from Southern England to Central Portugal. This typically Lusitanian distribution is illustrated by fig. 11. Doubtful records also exist for Switzerland and North Africa.

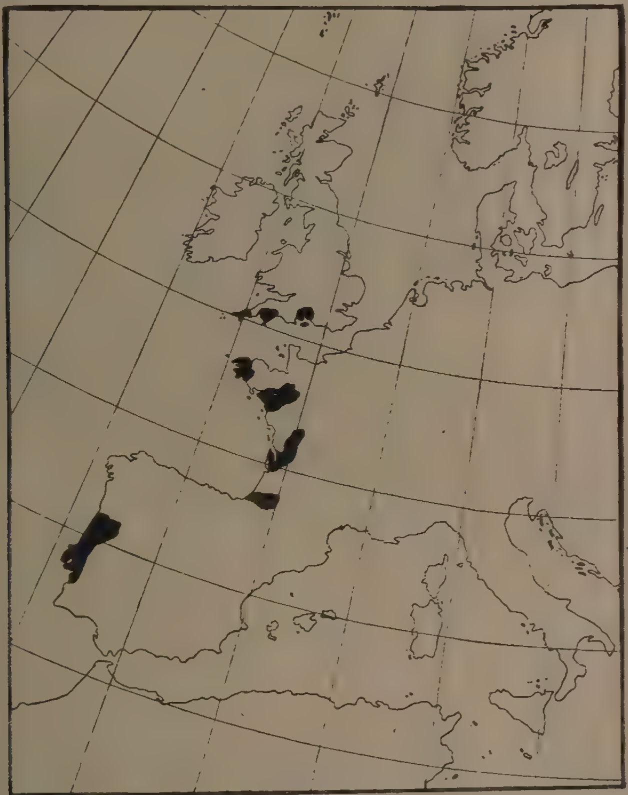

Fig. 11.—The established geographical range of *Dilta littoralis* (Wom.)

In Britain the known distribution is restricted to South-West England. In this locality Womersley (1930) obtained specimens from West Cornwall, South Devon and the Isle of Wight, and more recently the author collected them from South Hampshire.

With the exception of Argilas (1941) who found *D. littoralis* in Gironde, the remaining French records from the Departments of Finistère, Maine-et-Loire, Loire Inférieure, Charente and Basses-Pyrénées have been provided by Wygodzinsky (1941). He (Wygodzinsky, 1945) also collected this species in the Portuguese Provinces of Estremadura, Duoro Litoral and Beira Baixa.

Of the doubtful records Bär (1912) certainly obtained *Dilta* sp. from Switzerland but these were probably specimens of *D. hibernica*. The description by Lucas (1849) of *Machilis bimaculata* collected from North Africa possibly refers to *D. littoralis* (Wygodzinsky, 1945). Negative information on the distribution of this insect is difficult to obtain but the frequency with which the allied species, *D. hibernica*, has been found in Central and Northern Europe (Wygodzinsky, 1941) does suggest that these regions have been searched without success as far as *D. littoralis* is concerned.

2. The Areas Under Survey.

Two areas have been under survey.

The more detailed work has taken place on a strip of common land in South-East Devon (Grid. ref.: 30/08, 30/09) running South-West to North-East approximately 6 miles long and two miles wide and composed of Venn Ottery, Aylesbeare, Harpford, Colaton Raleigh, Woodbury, Bicton, Lympstone, East Budleigh and Withycombe Raleigh Commons. Geologically they consist of Lower Marls overlain by the Triassic, Budleigh Salterton Pebble Beds which to the North-East are covered by Upper Red Sandstone (Evans and Stubblefield, 1929; H.M.G.S., 1912). All the habitats subjected to detailed survey have been situated upon the rounded quartzite pebbles characteristic of the Pebble Beds. The remainder has been undertaken on a small patch of heathland one mile east of Lyndhurst, Hants., and known as White Moor (Grid. ref.: 41/31 3079) being situated upon the sandy, Oligocene, Middle Headon Beds.

The botany of the Devonshire commons has never been described, although reference has been made by Tansley (1939) to some unpublished work by Major on what appear to be similar vegetation types in Cornwall. The commons are a mixture of heath and grassland varying in altitude from 200 to 600 feet. The higher ground is dominated by the grass *Agrostis setacea* Curt. which appears to be the first coloniser after burning and is initially sparse in distribution. Invasion by *Calluna vulgaris* Salisb. may be at one of two stages, either before the *Agrostis* has become well established, i.e., relatively soon after burning, or when the *Agrostis* is fairly well established and then no lichens occur with the *Calluna*. This is in marked contrast with the frequency with which these plants occur among the stands of ling establishing themselves without the *Agrostis*. The latter appears to be a far more gradual process. A further, and lesser, factor permitting the introduction of *Agrostis* has been the influence of the military on the commons during the war. Instead of burning, the factors responsible for eliminating the vegetation have been the effects of explosives and heavy vehicles. Burning is a frequent phenomenon resulting in a large proportion of the commons being covered by *Agrostis*.

The *Calluna* is often, but not invariably, accompanied by *Ulex gallii* Planch., *Erica cinerea* L. and *Erica tetralix* L. At higher, better drained levels *E. cinerea* is slightly more abundant than *E. tetralix* while the reverse relationship occurs in the lower damper areas. Locally, the Callunetum becomes extremely well developed, attaining heights of as much as 60 cm., but it then tends to be invaded by *Ulex europaeus* L., with the formation of Ulicetum of still greater stature. True Ulicetum devoid of *Calluna* and *Erica* is of limited occurrence, found only as roadside patches and along embankments.

Stands of *Pinus sylvestris* L. of varying density occur sporadically succeeding both the Ulicetum and the Callunetum. Although natural regeneration is in process in various parts of the commons burning must considerably hinder its progress.

Molinia caerulea Moench. is present within the Callunetum but it is only on the lower, wetter ground that it attains its tufted dominance. Here, burning is still important but not to as great extent as on higher ground. With the *Molinia* occasional clumps of *Juncus communis* Mey. occur, and between the tufts in very wet localities, *Sphagnum*.

Pteridium aquilinum (L.) is sporadic, being absent from the very wet valleys and rarely becoming so dominant as to preclude the other vegetation. Beech plantations also occur.

The vegetation pattern of these commons is illustrated diagrammatically by fig. 12.

The work on White Moor, Hants., has not been as detailed as the foregoing. Suffice it to say that the area under detailed investigation was a stretch of heathland with *Calluna* dominating the higher ground and *E. tetralix* the lower ground which was inclined to be boggy.

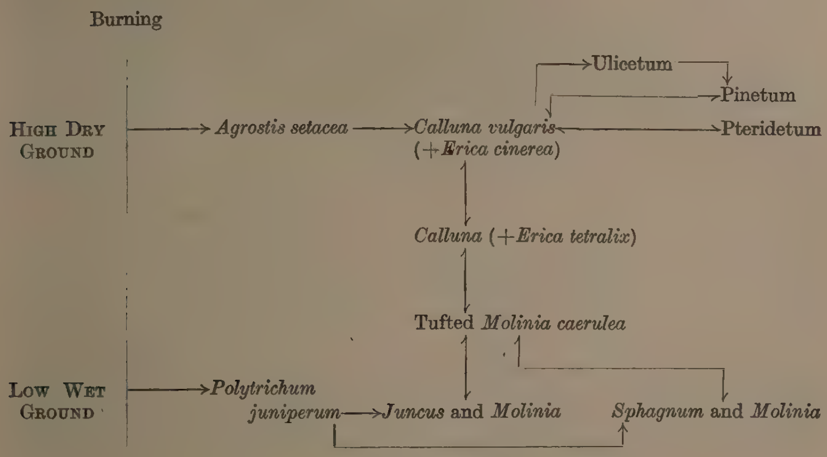
Burning
High Dry Ground
Agrostis setacea
Calluna vulgaris (+Erica cinerea)
Ulicetum
Pinetum
Pteridetum
Calluna (+Erica tetralix)
Tufted Molinia caerulea
Low Wet Ground
Polytrichum juniperum
Juncus and Molinia
Sphagnum and Molinia

Fig. 12.—The vegetation pattern of the commons in south-east Devon.

3. *Dilta littoralis* within the Plant Community.

Having now determined the nature of the various plant communities the next task is to relate vegetation type to presence or absence of *Dilta*. A number of different types of vegetation have been searched with varying degrees of success and the results are shown summarily below :

Date first searched.	Common.	Grid. ref.	Vegetation.	Present (P) or Absent (A)
13.x.50	V.O.	064916	Embankment of C. and A.	A
15.x.50	V.O.	065915	M. grassland	A
18.x.50	V.O.	067916	M., C., and E. on low moist ground	P
18.x.50	V.O.	067916	*Pt* on low fairly moist soil	A
18.x.50	V.O.	068917	Low dense C., 5–8 cm. high	P
18.x.50	V.O.	068918	C. and E. 15–20 cm. high	P
25.x.50	H.	048904	Pine litter	A
25.x.50	C.R.	043882	U. and C. 45–60 cm. high also M. and *Pi*	A
25.x.50	C.R.	042882	U. and C. 45–60 cm. high also M. and *Pi*	A
15.xi.50	W.	034864	Well developed U. and C.	A
15.xi.50	B.	044859	U. bushes 1·5 m. high	A
15.xi.50	B.	044859	C. 5–20 cm. high (B.C. III)	P
15.xi.50	B.	044859	Sparse C. 50 cm. high	A
15.xi.50	B.	044859	*Sphagnum* bog and tufted M.	A
24.xi.50	B.	034855	Low patchy C. with M., A., and U. (B.C. I)	P
24.xi.50	E.B.	038848	Dense C., U. and M. plus occasional *Pi*	P
24.xi.50	L.	025848	Needled floor of *Pi*	A
24.xi.50	E.B.	037848	M.	A
24.xi.50	W.R.	033841	Dense U., C. and E. 40–100 cm. high	A
24.xi.50	B.	034856	C., M., U., and A. 10 cm. high (B.C. II)	P
14.xii.50	B.	036851	Scattered C. interspersed with A.	P
14.xii.50	B.	033855	C., E. and M.	P
17.i.51	B.	033860	Early recolonising of burnt ground by A.	A
17.i.51	B.	036859	U. ground layer in Birch-*Pi* wood	A
17.i.51	B.	036859	C. ground layer in Birch-*Pi* wood	P
17.i.51	B.	036859	Needled floor of Birch-*Pi* wood	A
17.i.51	B.	034859	Low dense C., E., U. and *Cladonia* (B.C. IV)	P
7.ii.51	B.	042859	C., E. and M. on wet ground	P
7.ii.51	B.	036857	*Polytrichum*	A
7.ii.51	B.	041859	Very low C. (5 cm.) on wet ground	A
7.ii.51	B.	037857	*Juncus* and *Sphagnum*	A
7.ii.51	B.	042857	C. and E., 30 cm. high	P
26.ii.51	C.R.	057855	*Pt* and C., 23 cm. high	P
26.ii.51	C.R.	049888	Dense U., E. and C. (C.R.)	A
26.ii.51	C.R.	057884	Scattered patches of E. (10 cm. high)	A
26.ii.51	C.R.	057882	Burned ground without vegetation	A
28.ii.51	B.	031859	A. grassland with a little C.	A
16.vii.51	B.	045863	Beech wood litter	A
24.vii.51	W.	048865	A. grassland	A
24.vii.51	W.	048862	C., U. and E.	P

The names of the commons are represented by their initials and the plant genera by the first letter of the genus as used in the earlier descriptions of the areas; exceptions to the latter are for *Pteridium* and *Pinus* these being given by *Pt* and *Pi* respectively. The Grid. references have been taken from the 2·5 inch Ordnance Survey Sheet Nos. 30/08 and 30/09.

Although *Dilta* was not invariably present when *Calluna* was searched, *Calluna* was the only species always present in a plant association in which *Dilta* occurred. Pure stands of other plants contained no specimens and in consequence only the *Calluna* associations have been analysed further:

Plant genus.	Constitution of 16 *Calluna* habitats in which *Dilta* occurred.	Constitution of 7 *Calluna* habitats from which *Dilta* was absent.
Calluna (pure stand only) .	1	2
Molinia	6	2
Erica	8	2
Agrostis	4	1
Ulex	5	5
Pteridium	1	.

All species of plants, with the exception of *Ulex*, appear to be slightly more frequent in habitats favouring *Dilta*. In contrast *Ulex* is of markedly higher relative frequency in the associations from which *Dilta* was absent. Although favouring Callunetum, the insect was collected less often from stands of pure *Calluna* than when this occurred with other plant genera. As a result the more detailed studies have centred around various developmental stages of Callunetum and their mergence with other vegetation types.

It must also be appreciated that as only certain seres have been investigated it is quite conceivable that the insect may inhabit unsearched areas and live at a low population density in habitats from which it has been reported as absent. This is confirmed by specimens brought to the author from hawthorn hedgerows and beech and oak litters, and by Womersley (1930) who collected specimens from "amongst grass on the top of cliffs." The frequency with which the oak and beech litters are known to have been searched by other workers and the small number of *Dilta* resulting from them suggest the populations to be very low in these localities. Argilas (1941) collected large numbers from amongst pine needles; a habitat it has never been recorded from in Britain.

4. The Intra-Community Relationships.

Having examined the distribution of *Dilta* relative to plant communities it is now necessary to consider the pattern of the distribution within them. This involves the expression of plant communities in quantitative terms followed by an absolute estimate of the *Dilta* population inhabiting them. Whilst various assessments of absolute population density have been made (Ford, 1937; Varley, 1947) the methods referred to below, together with an attempt at correlating these quantitative assessments of both animal and plant communities, have not, to the author's knowledge, hitherto been used.

The preliminary work carried out in October and November, 1950, showed *Dilta* to be always present at the base of the vegetation and never in very large numbers. Of the quantitative methods available for the capture of these insects only trapping and hand collecting were operative. Marking and releasing experiments were considered inapplicable to an insect present in such small numbers. Trapping could have been undertaken but would not give absolute figures of population density. Whilst hand collecting is slow and tedious it can be a fairly accurate quantitative method if used in conjunction with a quadrat. The shortcomings of this method are obvious; it is for example quite possible that some insects, especially the smaller ones, will evade capture by being hidden in crevices amongst the herbage, the accuracy of the method depending upon the accuracy of the observer's eye. Under the circumstances, however, it was considered the more suitable method and was therefore adopted. Fifty half-metre quadrats were thrown, these being sufficient to give statistical significance and to permit the search of the vegetation they covered within one or two days.

So far, all that has been considered is the number of insects per 12·5 sq. m. (i.e., 50 quadrats) of substrate. From what has been stated above of the plant communities of the commons it is obvious that the nature of this substrate is subject to considerable variation and something rather more objective than a simple descriptive account of the nature of the vegetation is desirable when quantitatively determining an insect population which it supports. A satisfactory method, when one is considering the vegetation partly as a physical feature providing shelter for the Machilid, is an estimation of percentage cover together with mean height. As Ashby (1936) has pointed out, percentage cover estimations have certain limitations in quantitative ecology but serve well for the examination of gross changes in the composition of the community. As, for this work, it is only the gross features that are required, the method appeared quite satisfactory. Again fifty 0·5 m. square quadrats were thrown, but to obtain greater accuracy the quadrat was subdivided by means of string into twenty-five square decimetres; the mean height, a rough determination of stature, of each quadrat was determined with the aid of a ruler. In noting the percentage cover the observer stood with his head directly over the quadrat.

Five stretches of subjectively selected homogeneous vegetation were initially chosen for detailed study:

1. *Bicton Common I.* Grid. ref.: 30/034855. Fig. 13.—An area approximately 20 m. × 20 m. This area consited of *Agrostis* grassland in a moderately advanced stage of invasion by *Calluna*; the vegetation was very patchy, being interspersed with exposed areas of the underlying pebble beds. *Molinia* was also present. In view of the limited area of this habitat quadrats were not thrown randomly over the entire area but restricted to transects clearly demarcated at each visit, thereby avoiding the possibility of searching the same area twice.

2. *Bicton Common II.* Grid. ref.: 30/034856. Fig. 13. An area 50 m. × 30 m. This can be considered a more advanced sere than the above under slightly wetter conditions. The open space had diminished appreciably and the stature of the vegetation increased, in which *Ulex* and *Molinia* were playing increasingly important rôles.

3. *Bicton Common III.* Grid. ref.: 30/044859. An area 20 m. square. *Calluna* and pebble beds covered most of the substrate assisted to an almost negligible extent by *Erica, Molinia* and *Agrostis*. Owing to the small size of

the area, a certain lack of homogeneity existing in the vegetation pattern and an inadequate differentiation between this and the other vegetation types, this area was discarded.

4. *Bicton Common IV*. Grid. ref.: 30/034859. Fig. 13—A triangular area of approximately 2000 sq. m. This sera exemplifies the early encroachment of Callunetum (with a considerable amount of *Cladonia*) upon Agrostetum. There was very little open space in this habitat.

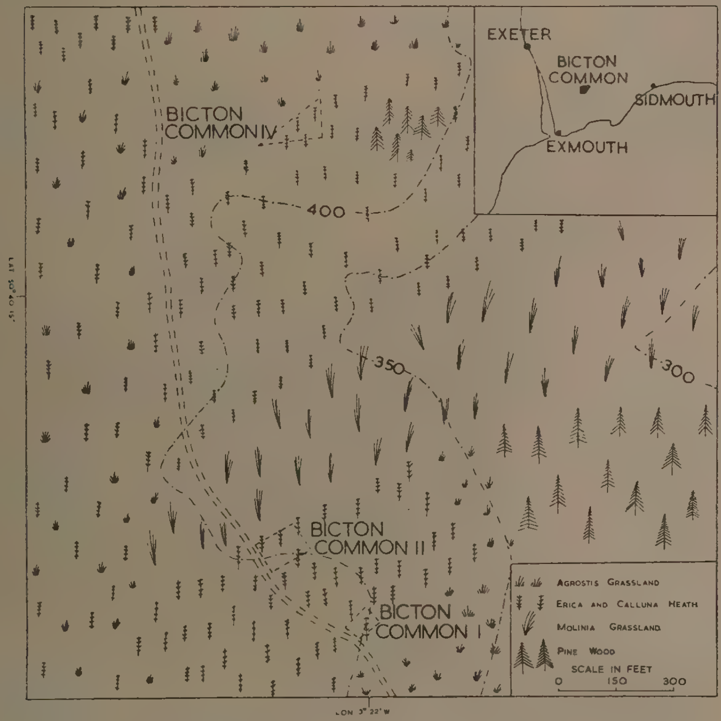
EXETER
BICTON COMMON
SIDMOUTH
EXMOUTH
BICTON COMMON IV
400
350
300
BICTON COMMON II
BICTON COMMON I
Agrostis Grassland
Erica and Calluna Heath
Molinia Grassland
Pine Wood
Scale in feet
0
150
300
LAT 50°40'15"
LON 3°22'W

Fig. 13.—Sketch maps showing the location and vegetation of the areas in Devon where population studies were made.

5. *Colaton Raleigh Common*. Grid. ref.: 30/049888.—An area 20 m. × 15 m. This area contrasted markedly with the others in the particularly dense *Ulex gallii*, which was the most abundant plant. The only way this could be efficiently searched was by the removal of the vegetation and instead of quadrats being thrown an area 12·5 sq. m. was cleared with a billhook. Either the effect of removing the vegetation or the unsuitability of the habitat was responsible for the absence of the insect. Two examinations (26.ii.51 and 21.v.51) revealed no insects and the habitat was not used further.

The percentage coverage of each genus of plant in these habitats was as follows:

	Calluna.	*Ulex.*	*Erica.*	*Molinia.*	*Agrostis.*	*Pinus.*	*Cladonia.*	Open.	Mean ht. of veg. (cm.).
Bicton Common I .	32·3	4·0	6·4	19·1	4·9	0·1	.	32·1	4
Bicton Common II .	35·1	14·1	11·1	25·0	4·7	0·1	2·3	7·5	10
Bicton Common III .	67·9	.	2·2	.	1·2	0·1	15·6	13·0	6
Bicton Common IV .	58·2	9·1	9·1	8·9	0·2	.	11·0	3·6	6
Colaton Raleigh Common . . .	26·2	39·2	31·7	1·5	1·1	.	.	.	32

The surveys were all carried out in the winter months but the habits of the heathland plants are such as to give little variation in percentage cover at different times of the year.

The three vegetation types worked had the following characteristics:

1. They were sufficiently distinctive to permit conclusions being drawn regarding differences in distribution of population that might be encountered.
2. They appeared to support a sufficient number of insects to provide some idea of the distribution of population throughout the year.
3. They were of such density and stature to be worked through by hand with a minimum of error.

The probability of throwing a quadrat in the same place twice seemed very improbable on Bicton Common II and IV in view of the large size of the areas under survey.

The method used was to throw the fifty quadrats, collect the animals from within each, and place them in a specimen tube. The actual capture is a simple procedure consisting of covering the animal completely with the tube and inserting the cork with a small amount of the accompanying substrate. It is rarely that *Dilta* is sufficiently agile to evade capture. The results of the analysis are shown below where they have been analysed by means of a Poisson distribution (Mather, 1949) to determine whether or not *Dilta* is randomly distributed and illustrated graphically by figs. 14–16. Fifty quadrats have been thrown except where stated to the contrary.

In Hampshire a sloping area of heathland was selected, on a sandy substrate, and falling approximately 25 ft. from dry *Calluna* and *Erica cinerea* to a dominantly *Erica tetralix* habitat. At each visit (January and August, 1951) a transect 15 m. wide and 115 m. long, the second parallel to the first, was marked out with the aid of a measuring tape, string and stones; running down the slope

Bicton Common I.

	24.xi.50.*	11.xii.50.	28.ii.51.	25.iv.51.	8.vi.51.	18.vii.51.	14.ix.51.	26.x.51.	29.xi.51.
Adults (born 1949) .	5	11	2	1	.	.	.	.	.
Juvs. (born 1950) .	15	15	14	5	1	.	.	.	.
Adults (born 1950) .	.	.	.	.	.	4	7	11	9
Juvs. (born 1951) .	.	.	.	.	.	16	35	42	23
Total . . .	20	26	16	6	1	20	42	53	32
Popn./Sq. m. . .	2·36	2·08	1·28	0·48	0·08	1·60	3·36	4·24	2·56
v/m . . .	1·8	2·92	2·09	1·58	.	1·63	1·92	4·46	3·36
$2\sqrt{\frac{2n}{(n-1)^2}}$ . .	0·54	0·41	0·41	0·41	.	0·41	0·41	0·41	0·41
Distribution . .	A	A	A	A	.	A	A	A	A

Bicton Common II.

	12.xii.50.	3.iii.51.	24.iv.51.†	14.ix.51.	16.xi.51.	11.xii.51.
Adults (born 1949)	3	1	1	.	.	.
Juvs. (born 1950)	9	5	1	.	.	.
Adults (born 1950)	.	.	.	7	6	9
Juvs. (born 1951)	.	.	.	19	19	9
Total	12	6	2	26	25	18
Popn./Sq. m.	0·96	0·48	0·27	2·08	2·00	1·44
v/m	1·50	1·40	.	2·06	1·90	1·83
$2\sqrt{\frac{2n}{(n-1)^2}}$	0·41	0·41	.	0·41	0·41	0·41
Distribution	A	R	.	A	A	A

Bicton Common IV.

	24.i.51.	23.iv.51.	9.iv.51.‡	20.vii.51.	12.ix.51.	12.xi.51.	7.xii.51.	22.ii.52.	7.vii.52.
Adults (born 1949)	6	2	2	.	.	.	.	.	.
Juvs. (born 1950)	23	13	18	.	.	.	.	.	.
Adults (born 1950)	.	.	.	4	14	17	11	10	.
Juvs. (born 1951)	.	.	.	1	38	33	18	11	.
Adults (born 1951)	.	.	.	.	.	.	.	.	22
Juvs. (born 1952)	.	.	.	.	.	.	.	.	24
Total	29	15	20	5	52	50	29	21	46
Popn./Sq. m.	2·26	1·20	1·60	1·25	4·16	4·00	2·32	1·68	3·68
v/m	2·00	1·70	1·60	1·20	1·41	2·80	1·64	1·45	.
$2\sqrt{\frac{2n}{(n-1)^2}}$	0·41	0·41	0·76	0·41	0·41	0·41	0·41	0·41	.
Distribution	A	A	A	A	R	A	A	A	.

A = Aggregative distribution. R = Random distribution.
* 29 quadrats thrown. † 30 quadrats thrown. ‡ 16 quadrats thrown.

and thus traversing the various types of vegetation mentioned above. At the uppermost level of each transect an area 10 m. × 15 m. was marked out and designated White Moor A, 25 m. along the transect a further area of 10 m. × 15 m. was marked out (White Moor B); similar areas appeared after stretches of 35 m. and 25 m. and were labelled White Moor C and D respectively.

The percentage cover and population of Areas A, B, C and D were estimated as in the Devonshire commons.

These were as follows:

	Calluna.	*Ulex.*	*Erica.*	*Cladonia.*	*Molinia.*	Water.	Open.	Mean ht. of veg. (cm.).
White Moor A	45·2	0·2	9·9	.	3·4	.	41·3	7
White Moor B	38·9	0·3	10·2	.	4·9	.	45·6	11
White Moor C	42·0	0·1	5·0	0·1	4·6	.	48·2	8
White Moor D*	9·7	0·2	21·0	0·1	.	0·9	35·6	7

* This includes 16·6 per cent. of a mat of vegetation composed of two species of *Carex* and a grass.

White Moor.

	A.		B.		C.		D.	
	20.i.51.	20.viii.51.	20.i.51.	21.viii.51.	21.i.51.	22.viii.51.	22.i.51.	23.viii.51.
Adults (born 1949)	.	.	1	.	2	.	6	.
Juvs. (born 1950)	7	.	15	.	6	.	48	.
Adults (born 1950)	.	7	.	9	.	4	.	10
Juvs. (born 1951)	.	28	.	39	.	33	.	33
Total	7	35	16	48	8	37	54	43
Popn./Sq. m.	0·56	2·80	1·28	3·84	0·64	2·96	4·32	3·44
v/m	1·79	1·83	3·40	2·20	4·70	2·00	2·30	2·50
$2\sqrt{\frac{2n}{(n-1)^2}}$	0·41	0·41	0·41	0·41	0·41	0·41	0·41	0·41
Distribution	A	A	A	A	A	A	A	A

Whilst areas A, B and C show little change in vegetation, D is particularly distinctive.

5. Discussion.

The behaviour of the populations as separate entities without any regard for the nature of the habitat from which they have been taken are considered first. Bicton Common I and IV (figs. 14 and 16) clearly support higher populations than Bicton Common II (fig. 15). It is noticeable, however, that whilst both these populations (I and IV) are at much the same level from September to December (1951), that of Bicton Common I drops considerably below that of Bicton Common IV from April to June. The three populations have the common feature of being at a maximum in September or October and from thence declining steadily until July. The attainment of a maximum in these months is obviously due to errors in the collecting technique as the life history studies indicate June–July, when egg hatching occurs, to be the period of maximum populations. The displacement is attributed to the very small size of the juveniles in July rendering them easily overlooked by the naked eye. In the case of Bicton Common I, the adult population is also unaccountably low throughout the summer months. It follows then, that the figures of the juvenile and total populations (figs. 14–16) would be more accurate if they ascended almost vertically at the time of hatching as the numbers of juveniles present at that time must at least equal their numbers later in the year. On Bicton Commons I and IV the generations born in 1949 and 1951 appear to have similar population densities in the two areas, but the 1950 generation is appreciably lower on Bicton Common I. The populations of Bicton Common II are lower for all generations than comparable ones elsewhere.

In Hampshire the most striking feature is the high population supported by White Moor D. In January it was at least three times as great as on any other known Hampshire habitat, whilst in the following August it was the second largest, being slightly below that of White Moor B. The smaller number of juveniles on White Moor D born in 1951 as compared to those of 1950 is of little direct importance, as being succeeding generations the former would be the progeny of the 1949 generation. This habitat differs markedly from the other portions of the Moor surveyed in having a much lower coverage of *Calluna*, a higher one of *Erica* and slightly less open ground, so producing a heathland under rather wetter conditions; no comparable habitat was investigated in Devonshire. There can be no doubt it produced conditions highly favourable to *Dilta*.

The earlier analysis for aggregation exhibits a predominance of this phenomenon, as is shown summarily below:

	Number of times aggregation occurs.	Number of times randomness occurs.
Bicton Common I	8	.
Bicton Common II	4	1
Bicton Common IV	7	1
White Moor	8	.

This may be due either to the selection of favoured microhabitats or the existence of some form of social habit, e.g., the laying of eggs in groups could

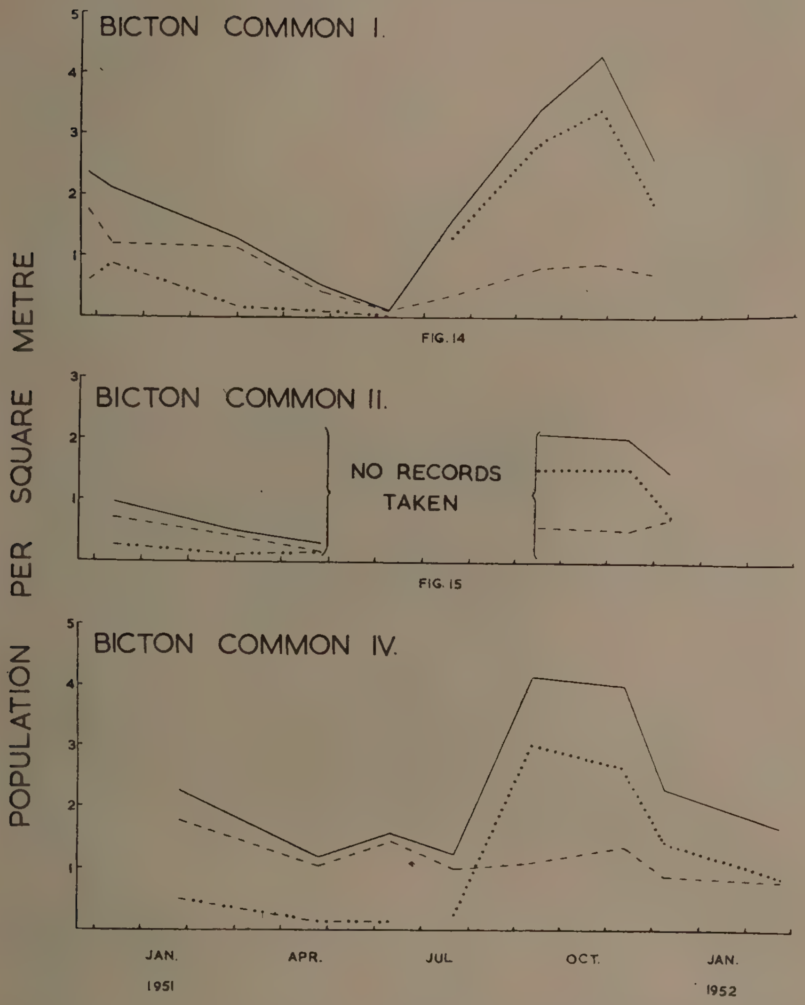

FIG. 14

FIG. 15

FIG. 16

FIGS. 14–16.—Population variations in the different areas of Bicton Common surveyed. The total population is represented by the unbroken line whilst its constituent populations hatching in 1949, 1950 and 1951 appear as dash-dot, broken and dotted lines respectively.

account for numbers of juveniles within close proximity. It has been shown above (pp. 44–45) that *Dilta* displays a preference for *Calluna* and *Erica* and the percentage coverage of these two species with that of open ground is shown below :

	Percentage coverage.			
	Calluna.	*Erica.*	*Erica* plus *Calluna.*	Open.
Bicton Common I . . .	32·3	6·4	38·7	32·1
Bicton Common II . . .	35·1	11·1	46·2	7·5
Bicton Common IV . . .	58·2	9·1	67·3	3·6
White Moor A	45·2	9·9	55·1	41·3
White Moor B	38·9	10·2	49·1	45·6
White Moor C	42·0	5·0	47·0	48·2
White Moor D	9·7	21·0	30·7	35·6

In White Moor D only 9·7 per cent. of the habitat is covered by *Calluna.* A 30 per cent. coverage by *Erica* and *Calluna* produces what appears to be the highest population density of all the habitats examined. On the basis of this either *Erica* or some other vegetation must be considered of equal importance to *Calluna* in supporting a population. In view of the mixture of the remaining third of the vegetation it appears improbable that much importance need be attached to it. Thus, in discussing further the distribution of *Dilta* in relation to vegetation, the cover provided by both the *Calluna* and *Erica* must be given prime consideration.

On Bicton Common IV over two-thirds of the ground is covered by *Calluna* and *Erica* and less than 4 per cent. is without vegetation. From this it follows that there can be little clumping of the plants while a closer approach to a random distribution is shown by the *Calluna.* This is not reflected in the population figures of *Dilta* for this habitat where only one, and this based upon sixteen quadrats, of the eight investigations showed a random distribution. In view of the large amount of open ground in the other habitats a certain amount of clumping of *Calluna* must result, and it is at this stage not possible to state categorically whether the aggregation of the insect in them is due to its association with vegetation or not. However, as a pointer to the possibility of grouping actually within vegetation, it has been noted that in the habitat showing least clumping (Bicton Common IV) the population of *Dilta* shows marked aggregation.

Because they have been subjected to more frequent estimation the populations of Bicton Common can be analysed with greater accuracy than those of White Moor. They have been placed in order of population density and accompanied by the coverage of *Calluna* plus *Erica*, the open ground and the remaining vegetation viz. :

	Percentage coverage.		
	Calluna plus *Erica.*	Open.	Remaining vegetation.
Bicton Common IV . . .	67	4	29
Bicton Common I . . .	39	32	29
Bicton Common II . . .	46	8	46

Although Bicton Common I supports a higher population than II, its coverage of *Calluna* and *Erica* is less. The relationship is not then a simple one between coverage of *Calluna* and *Erica* and population of *Dilta*. Bicton Common II has a greater quantity of other vegetation than I and IV and it appears that the combination of this with the *Erica* and *Calluna* has the effect of producing less favourable conditions. On Bicton Common II the vegetation is slightly taller than elsewhere (except White Moor B), which may also have an unfavourable effect, direct or indirect, on population density.

A correlation between population and vegetation in absolute terms would be of considerable value but is not practicable for several reasons. The major difficulties are the absence of a single plant species with which *Dilta* displays a really positive relationship and inaccuracies in the total population figures giving little more than a magnitude of accuracy. The above information illustrates the complexity of the factors, both direct and indirect, produced by different vegetation types and responsible for the maintenance of an insect population of low density.

V. THE EXTRINSIC FACTORS MAINTAINING POPULATION DENSITY.

Under this heading have been considered those factors, both density-dependent and density-independent, responsible for maintaining the population balance of *Dilta* but exclusive of those referred to by Chapman (1931) under the title of the biotic potential of the species. The following takes into account the food, associated fauna and physical factors as influences modifying population density and discusses the relative importance of each.

1. Food.

Full accounts of the anatomy of the Machilid alimentary tract as represented by *Machilis* and *Dilta* have been given by Oudemans (1888) and Argilas (1941) respectively. The gut of *Dilta* is composed of a straight tube with anteriorly a short slender oesophagus, posteriorly a short but rather wider rectum and medianly voluminous mid-gut containing food in course of digestion.

As the difficulties involved in observing feeding in the field were great, the food was largely determined by examining the gut contents of recently captured specimens. Having brought the insects back to the laboratory alive they were killed by piercing the head with a small entomological pin after the animal had been placed under water in a dissecting dish. A second pin was inserted in the posterior region, slightly anterior to the point of origin of the caudal filaments. With the aid of a pair of fine dissecting scissors a median dorsal incision was made through the body wall, the sides of which were then deflected to expose the alimentary system. The anterior pin penetrated the head capsule and was anterior to the gut and the posterior one penetrated the rectum. By cutting the oesophagus and rectum the gut was freed from major attachments and could then be removed to a microscope slide. Guts were examined as soon as possible after capture; this was usually after eighteen to twenty-four hours had elapsed.

One hundred and thirty-three guts have been examined and one hundred and twenty-five of these contained a greater or lesser amount of green material whose actual nature could not be determined using this technique. Structurally it consisted of a mass of minute green spheres occasionally aggregated in what appeared to be a gelatinous sheath. Superficially it appeared very similar to that illustrated by Oudemans (1888) in the gut of *Machilis*. The individual spheres were not uniform in size varying from 1 μ to 3 μ in diameter. Clearly, this extreme minuteness made structural determination exceedingly difficult. On the basis of its colour and size it was believed to have originated from a species of Chlorophyceae or Myxophyceae. A further examination of algae of the habitats from which *Dilta* had been taken showed the conjugate alga *Zygogonium ericetorium* Kütz. to be ubiquitous and easily the most abundant. The material in the alimentary tract was not, except on two occasions when cell walls were present, recognisable as *Zygogonium*, but owing to the inevitable delay in examination it was possible that the Alga was in an advanced state of digestion. In order to determine whether this was the major food two simple experiments were undertaken.

Experiment 1.—Eighteen insects were collected on 12.v.52 and kept without food at room temperature until 21.v.52. As a control five of their mid-guts were examined and each found to contain a small amount of the unidentified green material. The remaining thirteen were placed in a petri-dish whose base had been covered with *Z. ericetorium*; three of these were observed to feed at once. Of the thirteen guts examined the following day eleven contained recognizable *Zygogonium*, in many cases with fractured cell walls. This experiment at least illustrated the palatability of the alga to *Dilta* but it does not necessarily follow that the unidentified green material and *Zygogonium* are the same.

Experiment 2.—Twenty-eight insects collected 12.v.52 were starved at room temperature until 26.v.52. Five guts were examined and contained only green material. The remaining twenty-three individuals were offered *Zygogonium* and six of the ten examined the following morning had fed upon the alga. The remaining thirteen were removed from the alga and kept without food until the following morning (28.v.52), when their gut contents were examined. By isolating them in this way for at least twenty-four hours, conditions closely similar to those experienced in the course of a routine gut investigation were simulated. On examining the guts of the remaining thirteen individuals only a small number of empty *Zygogonium* cells were present in the hind gut of one individual, although a number were markedly full of the unidentified green material. The results of the first part of the experiment suggest it likely that more than 50 per cent. of the total insects, which includes those examined immediately after removal from the *Zygogonium* and those twenty-four hours later, have fed upon the alga. That the twenty-four hours of isolation from food is sufficient time for the insects to have defaecated or digested the diagnostic portions of the *Zygogonium* is inferred by the latter half of the experiment. These experiments support the view that *D. littoralis* feeds principally upon *Zygogonium* which has been digested beyond recognition when most of the routine examinations of the alimentary tract have been undertaken.

Sixty-two guts have contained *Zygogonium* exclusively; an analysis of the remaining seventy-one guts is set out below:

Material contained.	Number of specimens.
1. *Zygogonium ericetorum* Kütz. (always accompanied by at least one of the materials below)	63
2. Detritus	31
3. Soil particles	39
4. Arthropodan remains	
(i) *Dilta* scales	20
(ii) Hairs	4
(iii) *Dilta* exoskeleton	3
(iv) Unidentified exoskeleton	3
5. Bryophyte remains	
(i) Unidentified	9
(ii) *Sphagnum*	5
6. Angiosperm remains	
(i) Unidentified	10
(ii) Epidermis	4
(iii) Hairs	1
7. Algae (other than *Zygogonium*)	2

Detritus.—This consisted of unidentifiable organic material; dark brown in colour and comparable with detritus collected from the base of *Calluna* and *Erica.*

Arthropodan remains.—The basis for recognition was a piece of exoskeleton. The scales of *Dilta* could be readily identified; care was taken to ensure they were actually present within the gut and had not been scraped from the external surface of the animal during dissection. Quite a large percentage of the insects contained them and this is attributed to (*i*) the possibility that some may be scraped from the mouthparts at times of feeding and/or (*ii*) the habit of eating their own ecdysed exoskeleton. *Dilta* exoskeletons have been observed three times, being recognised by the presence of antennae, legs, scales, and abdominal segments. Their extreme thinness and absence of internal structure suggests that they were purely exoskeletal, dispelling the possibility, on this evidence, of cannibalism and suggesting the habit of eating their shed exoskeletons. This agrees with Denis (1949), who maintains that Machilids eat their shed exoskeletons except for the caudal filaments. He also states that whilst the exoskeleton is digested the scales are not.

Bryophyte remains.—The leaves of *Sphagnum* have a characteristic structure rendering them easily recognisable. The other remains are both leaf and stem and probably from *Hypnum* and *Dicranum,* as these are the only other common Bryophytes in the habitats populated by *Dilta.*

Angiosperm remains.—The unidentified remains were no more than groups of partly decomposed Angiosperm cells. The hairs correspond to those observed on *Calluna* and epidermal tissue was recognised by the presence of stomatal guard cells. These remains were frequently brown in colour.

Alga.—The unidentified alga appeared similar to *Chlorococcus.*

By staining with Sudan IV the mid-gut has been demonstrated to contain quantities of lipoid material.

In addition to *Zygogonium*, *Dilta* has been observed to feed upon *Sphagnum* in the laboratory.

This food is similar to the alga, lichens and vegetable debris of *D. hibernica*, *Trigoniophthalmus* and *Lepismachilis* (Wygodzinsky, 1941). This lack of specificity in *Dilta* is given stronger support by the frequency with which more than one food material has been found in the gut at one time. Argilas (1941) observed "*Pleurococcus* or a related genus" to be the major food of *D. littoralis*. It is conceivable that an alternative food was taken by his specimens which were collected amongst pine needles, a habitat in which *Dilta* was not found in this study.

Food as a factor limiting population density appears improbable as, not only is *Zygogonium* very abundant over all areas of the commons and heaths, except on recently burnt ground, at all times of the year, but also the variety of foods *Dilta* has eaten suggests that if this alga is absent alternative nourishment can easily be obtained.

From the nature of the gut contents as known, the site of feeding might be deduced. The presence of soil, detritus, *Zygogonium* and Bryophytes unanimously suggest the base of the vegetation of its habitat. This corresponds to the region from which the insects have been collected.

2. Associated Fauna.

Predators.—A brief survey of the animals associated with *Dilta* has been undertaken by quantitative hand collection of the larger species from the base of *Calluna* in those habitats where populations of *Dilta* have been estimated. Owing to the lack of direct evidence of the nature and extent of predation upon *Dilta* the full faunal lists are not included here but a list of the associated carnivores, which could on account of their size prey upon *Dilta* at some stage of their or its life history, has been appended. The composition of the individual habitats has varied with both locality and time.

Of an observed total of over thirty-five carnivorous species the more common ones were the Hemipteran *Nabis ericetorum* Scholz., the Coleoptera *Odontonyx rotundatus* (Payk.) and *Staphylinus aeneocephalus* Deg., the Chilopoda *Lithobius calcaratus* C. L. Koch and *L. lapidicola* Meinert, the Araneida *Clubiona* spp. *Erigone* spp., *Leptyphantes* spp., *Lycosa* spp., *Pisaura listeri* (Scop.), *Stemonyphantes lineata* L. and *Xysticus* spp., and the Opilionids *Oligolophus agrestis* Meade and *Phalangium opilio* L. In the field predation has only been observed by the presence of exoskeleton remains of *Dilta* on the sheet webs of *Stemonyphantes*. In the laboratory *Nabis ericetorum* and the spiders *Aranea diadema* L., *Trochosa terricola* Thor., *Lycosa* sp. and *Pisaura listeri* have all fed upon *Dilta*. It does not follow that these species will do so in the field, but in view of the abundance of spiders and the fact that *Dilta* is palatable to at least some of them it appears probable that they will, as Bristowe (1941) has suggested for the insect population as a whole, exert an important controlling influence over the *Dilta* population at all times of the year.

No vertebrates were actually seen in the areas surveyed, although five species were known to occur in adjoining habitats. Of these the more likely predators would be slow worms (*Anguis fragilis* L.,) lizards (*Lacerta vivipara* Jacq.) and shrews (*Sorex araneus* L.).

Parasites.—An unidentified cephaline Gregarine has been the only parasite observed in *Dilta*, having been restricted to its alimentary tract and occurring at all developmental stages of the host. Of the sixty-two tracts examined, the parasite has been observed in numbers varying from one to one hundred and twenty-five in thirty of them. No previous records of parasitisation of *Dilta* have been recorded, although Denis (1949) has stated parasitic infections by Gregarines to be common within the Machilidae.

3. Physical Conditions.

The problem of determining the effect of physical conditions on the population of *Dilta* has been approached from two aspects. These have involved the measurement of the microclimate, as represented by temperature and humidity, in the field as well as a determination of the tolerance of the insect to controlled laboratory conditions.

The microclimate of pioneer *Calluna* up to 20 cm. high and from which specimens of *Dilta* have been taken has constituted a study in itself (Delany, 1953*b*). It may be summarily stated that in the course of measuring microclimate on several days of varying climatic conditions the effect of *Calluna* was to produce a more equable climate at its base than was found at the surface of adjoining exposed ground. The maximum and minimum temperatures of uncovered ground were 32·5° C. and 2·8° C. respectively, whilst those at the base of *Calluna* for the same periods ranged between 24·25° C. and 3·1° C. The humidity was variable but tended to be higher and less variable at the base of the vegetation than at higher levels within the plant cover and over the surface of exposed ground.

The apparatus used in the laboratory experiments on tolerance to temperature and humidity was based upon that described by Buxton and Mellanby (1934). It consisted of a glass jar 3·5 in. high and 2 in. diameter containing five uncorked 0·375 in. × 2 in. specimen tubes held vertical by a padding of glass wool around their bases. With their glass lids in place the jars enclosed an airtight system A constant humidity was maintained with KOH solutions of various concentrations. Buxton and Mellanby (1934) give the relationships between relative humidity and specific gravity of KOH solutions and it is upon these figures that this work has been based. Relative humidities at 10 per cent. intervals from 50 per cent. to 100 per cent. have been used. Each jar contained 30 c.c. of solution and in each tube was placed one animal, thereby avoiding any effects of overcrowding. This apparatus was used at each of a series of experimental temperatures, except 15° C. when desiccators containing 2 in. × 1 in. specimen tubes were used instead. Although the solutions gradually crept up the outside of the tubes, frequent cleaning prevented them reaching the animals. Constant temperature was maintained at 4° C. and 21° C. using a thermostatic cabinet combining both heating and cooling units. An oven was used for maintaining temperatures of 27° C. and 35° C. and a cellar for 15° C. To permit the establishment of an even humidity on transferring the jars from one temperature to another, they were left at least three days in the new temperature before introducing any insects.

Dilta was unable to ascend the walls of the tubes, thus rendering any form of cover unnecessary.

Ten insects were set up at each humidity and their mean length of life determined. Examinations were made daily at all temperatures except 35° C. when they were made hourly. At lower humidities the insects lost water and appeared shrunken just prior to death whilst at higher ones they distended considerably. Owing to the sparse stock of animals available it was not possible to commence all the experiments simultaneously although enough specimens could be collected within one or two days to set up a series of experiments at one temperature for all humidities. Only juveniles were used in these experiments, all of them being collected between August and December, 1951. The insects were placed under experimental conditions two days after capture. That these insects were starved is of little importance as the experiments only attempt to determine the conditions most suited to the animal and are not concerned with longevity. The relationship between length of life (days) and humidity at various temperatures is shown below :

Temperature (° C.).	Relative humidity (per cent.).						Month Collected (1951).
	50.	60.	70.	80.	90.	100.	
4 ± 2 . .	9·4	8·0	11·1	11·6	12·8	44·1	October
15 ± 2 . .	.	8·8	8·2	14·3	18·2	21·9	August
21 ± 1 . .	3·6	5·6	8·1	10·4	12·4	11·2	November
27 ± 1 . .	3·6	4·6	7·9	8·9	9·3	16·0	September
35 ± 1 . .	0·4	0·5	0·7	0·8	0·8	0·9	December

These results indicate a much longer survival at the higher humidities, particularly at the lower temperatures. As the animals used in these experiments were of uniform age for one temperature only, comparisons between life length and temperature at constant humidities cannot be applied too rigidly. At maximum humidity (100 per cent.) a low temperature appears optimal but at lower humidities (80 per cent.–90 per cent.) a somewhat higher temperature (around 15° C.) is favoured. The figures strongly suggest the optimum experimental temperature to lie between 4° C. and 15° C. for all humidities. At 35° C. temperature exerts an influence so dominating as to produce only 0·5 days difference in life length between the lowest and highest humidities.

In comparing these figures with the field measurements of microclimate it must be remembered that the insect under field conditions is experiencing fluctuations in temperature and humidity which the laboratory animal is not. The highest temperature measured at the surface of exposed ground was 34° C. but it is probable that on hot summer days temperatures higher than this are experienced for periods of several hours and under such conditions, in order to survive, *Dilta* would be forced to remain within the vegetation cover. Although for the most part conditions outside the vegetation appear tolerable to the insect those within it approximate closer to the optimal conditions observed in the laboratory. Little is known of the tolerance limits at lower temperatures. After a night of severe frost in the winter of 1951 a dead *Dilta* was collected from the base of *Calluna*. On no other occasion was it possible to check this observation, but the absence of any bodily mutilation of the dead animal found suggests that it may have been killed by low temperature.

VI. Discussion.

This study of *Dilta littoralis* delineates certain aspects of its life history and ecology and exemplifies the existence of an insect at a constantly low population density. This latter feature is true of most of the other species of the same size found within pioneer *Calluna*, the fauna of this habitat being relatively poor in numbers and species.

Although distribution can be correlated with vegetation pattern, no direct relationship has been detected between *Calluna* or any other flowering plant and the population of *Dilta*. It follows that the combined interaction of the climate, the particular type of macro-vegetation, the soil and the previous history of the distribution of the species are the conditions responsible for the existence of a population. As *Zygogonium* occurs in regions from which *Dilta* is absent, these conditions are not simply those optimal to the food.

The factors controlling population density fall into two groups, those favouring increase and those favouring decrease. The former embraces the biotic potential of the species which in *Dilta* includes its rather low reproductive capacity and the existence of cryptic colouration. The assessment of fecundity suggests that each female lays on average fifteen eggs and it is highly probable that not all those will survive the winter and hatch the following spring. If the population is to maintain an even balance approximately two or three eggs produced by each female must survive the two developmental years. Starvation can be disregarded as a limiting factor, as food has invariably occurred in quantity. Predators probably constitute the major population control, as evidenced by the absence of other effective controlling factors and the relatively large numbers of carnivorous species collected at various times of the year.

It has not been practicable, however desirable, to determine the quantitative effects of predators as a group or as individual species. The difficulties involved in this problem are particularly numerous and when it is considered, for example, that such carnivorous forms as spiders contain no recognisable gut contents, are generally not highly specific feeders and in certain cases, e.g., Lycosidae, Thomisidae, have no webs on which skeletal remains could appear, a quantitative exposition of predator-prey relations presents itself as a problem of vast scope and considerable duration. The populations undergo their heaviest mortality from mid-summer to early autumn when at a maximum following the summer hatchings. This is probably due to the increased numbers and activity of the associated predatory fauna at the same time.

Climate, as has been stated previously, exercises slight control over population.

The outbreaks of fires on the commons usually last several hours and, less frequently, days. If they extend to the Callunetum, surface vegetation and fauna are completely destroyed. The roots of the plants are generally able to survive and very short *Calluna* shoots with those of *Agrostis* appear soon after burning. Whilst the vegetation may re-establish itself in this manner the fauna, including *Dilta*, must for the most part be introduced from surrounding unburnt areas. The eggs of *Dilta* have not been found in the wild and it is possible that some may be sufficiently secluded to escape the effects of light burning. If movement or transport of *Dilta* is not rapid (no experimental evidence of this exists) or, alternatively, if large areas of heath have been burnt, it is likely that the developmental growth of *Calluna* will outpace the rate of spread of *Dilta* and result in the production of a habitat which would apparently otherwise support a population but does not. Whilst predator control is density-dependent in its operation, climate and burning are density-independent, the latter resulting in the severest condition of extermination.

VII. Appendix: a List of the Carnivorous Species Associated with *Dilta littoralis*.

1. Species resident in the same habitats as *Dilta*:

Hemiptera:

Nabis ericetorum Scholz.

Coleoptera:

Amara famelica Zimmerman.
Calathus melanocephalus L.
Nebria brevicollis (Fabr.).
Notiophilus aquaticus (L.).
N. palustris (Dufts).
Odontonyx rotundatus (Payk.).
Philonthus fuscipennis (Manner.).
Staphylinus aeneocephalus Deg.
Tachyporus hypnorum (Fabr.).
Xantholinus longiventris Heer.

Diptera:

Various unidentified larvae.

Myriapoda:

Lithobius calcaratus C. L. Koch.
L. lapidicola Meinert.
Schendyla nemorensis C. L. Koch.

Araneida:

Aranea diadema L.
Clubiona diversa Cambr.
C. trivialis Koch.
Erigone promiscua Cambr.
Leptyphantes obscurus Bl.
L. sp., probably *leprosus* Ohl.
Lycosa picta Hahn.
L. saccata (L.).
Oxyptila sp. juvs.
Pisaura listeri (Scop.).
Stemonyphantes lineata L.
Tegenaria sp.
Theridion bimaculatum L.
T. denticulatum Walck.
Tibellus oblongus (Walck.).
Trochosa terricola Thor.
Xysticus audax (Schrank).
X. cristatus Clerck.
X. ulmi (Hahn.).
Indeterminable juveniles.

Opilionidea:

Oligolophus agrestis Meade.
O. hanseni Kraep.
Phalangium opilio L.

Crustacea

(Feeding habits in some doubt.)

Philoscia muscorum Scop.
Porcellio ratzeburgii Latr.
P. scaber Latr.

2. Species which may periodically visit habitats populated by *Dilta* although only observed in adjoining ones :

REPTILIA ;

Anguis fragilis L.
Lacerta vivipara Jacq.
Natrix natrix L.
Vipera berus (L.).

MAMMALIA :

Sorex araneus L.

VIII. SUMMARY.

1. The life history studies suggest the maximum longevity of females of *Dilta littoralis* (Wom.) to be just under two years ; that of male is slightly shorter. Approximately 15 eggs are laid by each female in July–August, the majority hatching the following June and July. Growth is rapid during the summer months and virtually at a standstill from late September to the end of May ; during this period there is no indication of hibernation. For the latter twelve months of their life the females are slightly larger and more numerous than the males. The ratio of males to females is variable within narrow limits.

2. The phenomenon of annual cyclic isolation has been observed in *Dilta* and its occurrence in other species of Machilidae discussed.

3. The geographical distribution of *D. littoralis* as known is typically Lusitanian.

4. The percentage cover provided by the plant genera in three areas of heathland in Devonshire and four in Hampshire has been estimated with the aid of ½ m. square quadrats and the population of *Dilta* in the former determined by collecting the animals present within known areas at intervals over twelve months period. These results are compared with the only population estimates made in Hampshire in January and August, 1951. Populations have been found to be at a maximum from August to December and at a minimum from April to June. The figures obtained have been analysed by means of a Poisson distribution and indicate the insect to be almost invariably aggregated. The reasons for this have been discussed and it has been suggested that it is not due solely to aggregation of the vegetation *Dilta* inhabits. *Calluna* has been the most favoured plant, whilst *Erica* has also been found tolerable to the insect. The existence of *Molinia*, *Ulex* and *Agrostis* with *Calluna* and *Erica* appear to produce less favourable conditions than if the area covered by the former were open ground.

5. By examining the gut contents of 133 insects and by conducting laboratory experiments, it has been inferred that *Dilta* is a vegetarian-detritus feeder with conjugate alga *Zygogonium ericetorum* its major food.

6. Of the carnivorous animals associated with *Dilta*, Araneida have been the most abundant. A cephaline gregarine has been found in the gut of about half the insects examined.

7. Climatic conditions at the base of *Calluna* where *Dilta* lives have been measured. They display greater uniformity of temperature and higher and

greater uniformity of humidity than open ground where vegetation fails to exercise any influence. In the laboratory *Dilta* has shown a preference for high humidities, particularly at lower temperatures, by displaying greater tolerance to these conditions.

8. The qualitative effects of the factors controlling its population density have been discussed.

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Vol. 105. Part 4. Pp. 65–77. 5 plates, 3 figs. 11th May, 1954

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NOTES ON THE BEHAVIOUR OF SWARMS OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSKÅL) DURING OVIPOSITION IN IRAN.

By G. B. Popov, M.B.E., F.R.E.S.
(*Desert Locust Survey.*)

Manuscript received 27th October, 1953.
(Read 4th November, 1953.)

With 5 Plates and 3 Text-figures.

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Introduction.

Although laying swarms of the Desert Locust (*Schistocerca gregaria* Forskål) are frequently seen by locust officers, such observations usually remain unpublished, probably because of their disjointed nature.

During the period from 12th December, 1950, to 10th June, 1951, the author saw several laying swarms in the course of his work as a liaison officer with the Iranian Locust Control Organisation in southern Iran. Unfortunately, the demands of control work prevented a continuous and more detailed study, but such observations as it was possible to make are discussed in this paper in the hope that they may fill some gaps in the published data on the subject. General notes on the country and the locusts will be found elsewhere (Popov, 1953).

This work owes much to the suggestions and encouragement received from Dr. B. P. Uvarov, Mr. P. R. Stephenson, Dr. R. C. Rainey and Miss Z. Waloff.

1. Influence of Reproductive Activity on the Composition of Swarms.

Segregation of Mature and Immature Locusts.

The degree of maturity of the swarms seen during the period under discussion varied; earlier swarms seen in December, 1950, were immature, while swarms seen at later dates comprised a mixture of mature and immature locusts and still others were wholly mature (Table I).

TABLE I.—*List of observations.*

Obs. no.	Date.	Locality.	Lat. N.	Long. E.	Degree of maturity.	Proportion of sexes (♂♂ : ♀♀)
–	18.xii.50	Ginau	27° 8′	56° 17′	Immature	153 : 147
–	20.xii.50	Rizwan	27° 35′	56° 00′	,,	68 : 76
1	22.ii.51	Sabzevaran	28° 37′	57° 53′	Mature	Roughly equal.
2	23.ii.51	Deh Luran	28° 18′	57° 48′	Mixed	,, ,,
3	25.ii.51	Kahnuj	27° 58′	57° 45′	Mature	,, ,,
4	25.ii.51	Muri Kurdi	27° 52′	57° 35′	,,	?
5	25.ii.51	Kahnuj	27° 58′	57° 45′	Egg-site	–
6	8.iii.51	Manujan	27° 25′	57° 32′	,,	–
7	25.iii.51	Tashkurd	28° 07′	56° 38′	Mature	About 50 : 1
8	10.iv.51	Gudar-i-Chorm	27° 55′	56° 02′	Egg-site	–
9	22.v.51	Pul-i-Nasiriyeh	30° 22′	56° 12′	Mixed	♂♂ slightly outnumbering ♀♀.
10	31.v.51	Gudar	29° 45′	57° 17′	Mature	?

The terms "mature" and "immature" are used somewhat arbitrarily in this paper, in the following senses: an immature swarm is one composed of individuals all of which are pink; a mature swarm is one in which all the individuals are yellow; and maturing and mixed swarms are those that may be composed of immature adults which are still partly or completely pink, wholly mature, yellow adults which engage in mating and laying during the course of the observation, and yellow adults which for various reasons do not engage in reproductive activity and which may either attend the fully mature laying and mating locusts, or follow the immature ones. In the case of a mixed swarm that splits into two parts, one largely composed of immature and the other of mature individuals, the two parts, now forming two separate units, are referred to as immature and mature, regardless of a proportion of yellow adults, which are in fact neither wholly mature nor wholly immature.

When the immature locusts in a mixed swarm were in relatively large numbers, their morning behaviour-sequence leading to departure followed the pattern described by Gunn *et al.* (1948), Kennedy (1951) and Waloff and Rainey (1951). Such a swarm, composed of yellow and pink adults in about equal numbers, was seen at Deh Luran (Obs. 2). It approached shortly before sunset and settled on the trees and bushes for the night. None of the locusts settled on the ground on arrival, and none descended to it until the following morning. Their activity during the next morning is represented diagrammatically in fig. 1. The first activities after sunrise (06.15 hr.) were crawling, basking and partial descent to the ground. By 07.15 hr. locusts were flying to the ground in numbers to continue basking on the bare patches of ground, while others flew about over short distances, singly or in little groups (this being the milling and surging of the quoted authors). At 08.10 hr., streaming began; it was initiated by those on the ground, and those in the trees joined the stream when it approached them. By 08.30 hr., stream-away was general, and the air was full of locusts flying close to the ground in a common direction to the south, at right angles to the sun, and in calm air. The roosting site was rapidly evacuated soon after 09.00 hr., except for about one-third of the population, comprising the mature individuals, which remained on the ground without showing much response to the departure of the rest.

There was no feeding before take-off, but after flying southwards for two miles, the swarm settled and began feeding on patches of annuals. This supports the suggestion made by Waloff and Rainey that feeding may inhibit flight at times, even when weather conditions are conducive to sustained flight. The feeding ended at 10.30 hr. in a sudden, spectacular mass-departure, the impulse for which appears to have been a sudden light breeze. No copulation was observed during the feeding period. The final departure of the swarm was complete, there being no stragglers left behind at the feeding site.

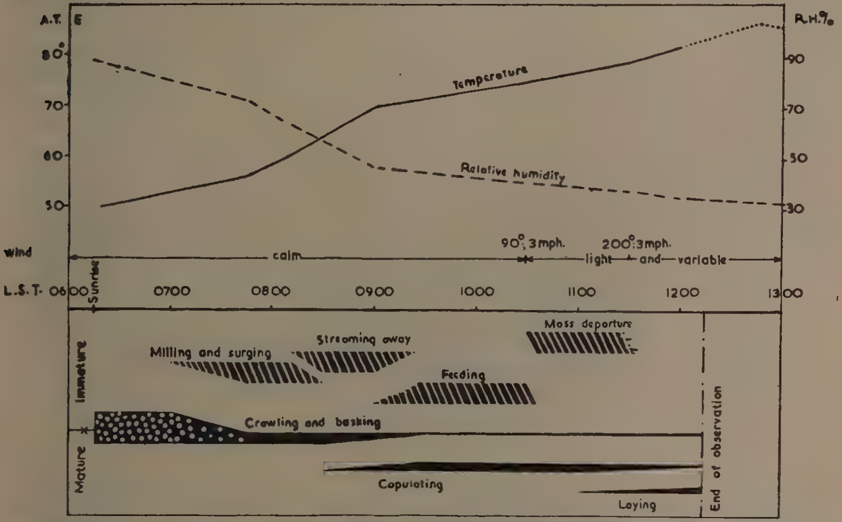

FIG. 1.—Obs. 2. Activities of locusts in a swarm composed of mature and immature individuals on the morning of 24.ii.51. Each form of activity is represented by a stripe, the width of which is based on a visual estimate of the relative proportion of locusts engaged in that activity and not on actual calculation of the numbers involved. Mature locusts are indicated by solid black stripes, immature ones by black barred with white, and the mixture of the two before segregation by black speckled with white.

Only the initial activity of crawling and basking was shared by all the locusts comprising this swarm. Afterwards, while the immature locusts were leaving the roosting site, the mature ones continued to bask and crawl; they were finally left behind, and at 08.30 hr. they began to copulate prior to laying. Most of them were pairing by 09.30 hr., but occasionally during the earlier part of this period, a couple would interrupt mating and follow the departing stream of other locusts. The remaining scattered pairs gradually collected into groups, mainly along the shallow sandy runnels, and the first laying was recorded at 11.00 hr. A small number of locusts, however, mainly males, took no part in the mating and continued to bask throughout the period of observation.

Thus, segregation was effected by differential behaviour. It appeared that the reproductive urge of the mature locusts overcame the tendency towards flight, while the latter dominated in the immature ones. This was also demonstrated on another occasion (Obs. 1), when numerous locusts differing in maturity and flying from ground level to a height of about 50 feet passed directly over a site occupied by mating and laying locusts at 10.30 hr. The fliers passed without stopping and none of the locusts on the ground showed any visible response to them.

When the number of immature locusts in a mixed swarm is relatively small, their behaviour may be influenced by the more numerous mature individuals. Obs. 9 (figs. 2 and 3) is a case in point. Here the swarm, consisting of over 90 per cent. yellow and the rest pink individuals, arrived at dusk and settled for the night. By the following afternoon, the mature locusts had paired and formed isolated groups, while the immature ones were segregated at the northern extremity of the area occupied by the swarm and there formed loose concentrations on the taller bushes. On the following morning, the immature locusts were seen at the same site, roosting and feeding ; no spontaneous flights were observed, but they were very active and flew readily when approached.

Swarms engaged in reproductive activities often included many individuals that did not participate in them. These individuals sometimes represented an immature minority such as that described above (Obs. 9), and sometimes a surplus of individuals of either sex. Occasionally, however, yellow locusts of both sexes were present but not pairing. The reasons for this inactivity were not ascertained, but may have been delay in maturation or sexual exhaustion. A case of mature locusts of both sexes (but largely males) failing to participate in the mating and laying activities of their fellows, and engaging instead in prolonged crawling and basking, was seen in the course of Obs. 2 (fig. 1).

Sex-ratio in Swarms.

The earlier observations suggested that in the immature swarms, the two sexes were usually in roughly equal proportions. A random sample taken from an immature swarm north of Bandar Abbas in mid-December, 1950, was found to consist of 153 males and 147 females ; another, taken a week later from a similar swarm at Rizwan, was composed of 68 males and 76 females.

The causes of the small disproportion of sexes that occasionally occurs in immature swarms are unknown. No evidence has ever been collected on the proportion of sexes at the final moult of hopper bands, or on the rate of mortality of immature males and females, or their rate of development in the field.

Much greater divergence in the sex-ratios was noted with the onset of maturation. The initial cause appears to be the faster maturation of the males in a swarm. Hynes (1946), in his field observations on locusts in Somalia, speaks of a gradual maturation, recognising a definite sequence in the yellowing of the body-parts in the two sexes of the Desert Locust. Thus, " first the shanks of the hind legs of the males, then the wings of the males, then the shanks of the females, followed by the heads, thoraces, and abdomens of the males. The females then go yellow in the same way as the males, but the abdomens of females remain red for some time after the rest of the body has gone yellow." The author further claims that, " Because of this definite order of events it is possible to tell whether a swarm that is mixed is a mixture of red and yellow swarms, or whether it is merely turning yellow—if red males and yellow females are present, it is definitely of mixed origin." This view finds further support from laboratory observations by Norris (1952), who records that the maturation of females follows that of the males and never precedes it. Observations in Iran agreed closely with the findings of Hynes.

Because of this difference in the rate of maturation of the sexes, it may be expected that during the segregation of mature and immature adults, a greater number of males than females would remain in the static (mature) portion of the swarm. This appears to have been the case in Obs. 2, as was shown by the predominance of the unmated males after the departure of the immature adults. Conversely, on the assumption of initial equality of sexes in a swarm, the females would predominate in the dynamic (immature) portion.

When locusts of the predominant sex were numerous, those that were surplus sometimes formed separate swarms and flew away, leaving those that were mating and laying behind. This happened in a swarm seen at Tashkurd (Obs. 7) ; the males outnumbered the females by fifty to one and when the vast majority of females had paired off, most of the surplus males were in flight, drifting away from the rest of the swarm. Thus, the swarm split into two parts, one being formed by males and the other with the sexes in nearly equal numbers. The predominance of males may have been due not only to segregation of the sexes, but also, and to an even greater extent, to the females dying first, as was suggested by dead, predominantly female, locusts found at this site. Another example of this was seen during Obs. 10. Here the swarm had remained settled at the oviposition site for some ten days. The ovaries of most of the females seen were exhausted and the area was littered with dead females. By comparison, the males were much more active and there were few dead males. Hynes (1946) also records the earlier death of females and speaks of swarms almost entirely composed of males towards the end of the oviposition period.

There thus appears to be considerable variation in sex-ratio during the life of maturing and mature swarms. There are probably many reasons for this in addition to those mentioned above. Considerable reserve is needed, therefore, in the interpretation of records of sex-ratios, unless the history of the swarm concerned is known.

2. Reproductive Activities.

Locusts were observed copulating and laying over a fairly wide range of conditions (Table II). Since, during the period of reproductive activity, most of their time is spent on the ground, the micro-climate at the soil surface, including radiation and the temperature, humidity and composition of the soil itself, might be expected to influence behaviour. Unfortunately, it was only possible to measure the air temperature and the relative humidity at a height of three feet above ground with a whirling hygrometer. The data so obtained are given in Table II, and figs. 1 and 2 illustrate Obs. 2 and 9. Some general notes on sunshine and the strength of wind were also made, but the wind did not appear to have any noticeable effect on the reproductive activity (fig. 2).

Mating.

In Obs. 2, mating began at an air temperature of 64° F. (Table I ; fig. 1) and roughly corresponded to the start of the vigorous flying activity of the immature adults in the same swarm. Once mating had begun, the couples remained united even when conditions became unsuitable for other forms of activity. Thus, in Obs. 9 (fig. 2) the locusts were found already mating at sunrise (A.T. 63° F.) and it was probable that they had spent the night *in copula*. At midday, when the air temperature rose to over 90° F., the couples sought shelter in the shade of plants, but came out again when the sky became overcast, though the air temperature dropped only one degree. Locusts were still mating at 23.00 hr. (A.T. 75° F.). In all recorded cases, mating preceded laying and on two occasions (Obs. 9 and 10) when the termination of laying was observed, copulation occurred again.

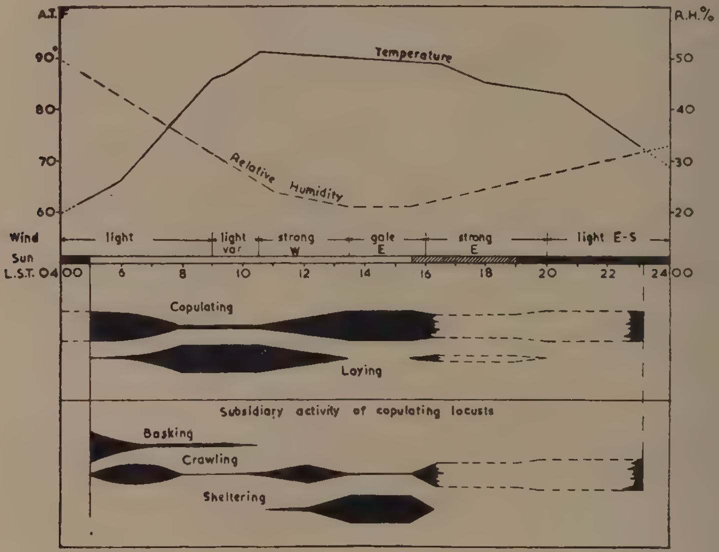

Fig. 2.—Obs. 9. Activities of locusts engaged in copulating and laying on 24.v.51. (The activities are indicated as in fig. 1.)

The period between the commencement of mating and that of laying varied. Obs. 1 and 2 are similar in that mating began in the morning and laying at midday or in the early afternoon. On the other hand, in Obs. 3, 5 and 9, mating apparently continued throughout the first day but laying did not occur until the following morning. During the period of mating and until the beginning of laying, the paired locusts exhibited other forms of activity also (fig. 2). This took the form of basking, crawling, sheltering and feeding. In all these subsidiary activities, the initiative was apparently taken by the female and the male was merely transported; in Obs. 10, even feeding was almost entirely confined to females.

Laying.

Although the initial probing was once seen at 63° F. (Obs. 9), mass oviposition was restricted within a temperature range of 72° F. to 92° F. (Table II).

Table II.—*Temperature and air humidity conditions at the time of mating and egg-laying.*

Obs. no.	Date.	Local time.	Air temperature (° F.).	Air humidity (per cent).	Activity of locusts.	Remarks.
1	22.ii.51	10.50	72	69	Copulating but not laying	Pairs crawling about and beginning to concentrate in loose groups.
		16.00	74	45	Laying in dense groups	Laying on sunny slopes and banks; orientated at right angles to sun.
2*	24.ii.51	08.30	64	58	Beginning of mating	Majority orientated at right angles to the sun. Laying believed to have continued without interruption at mid-day.
		11.00	77	38	Beginning of laying	
3	26.ii.51	11.30	78	35	Half of the swarm laying	Collecting in shallow hollows, others scattered about.
7	27.iii.51	15.00	76	22	Laying	In small dense groups.
9*	24.v.51	05.00	63	46	Mating	Collecting in groups, some probing the ground.
		08.00 10.30	78–92	35–24	Mass laying	Very dense groups.
		13.30	91	21	Laying suspended	In shade of bushes, some crawling about in the open. Bright sun.
		15.30	89	21	Laying resumed	Cloudy and dull.
		23.00	75	31	Mating	Pairs crawling in the open.
10	31.v.51 to 3.vi.51	–	72 to 81 (max.)	36 (av.)	Regular laying	Continued daily egg-laying within indicated temperature range.

* See corresponding graphs (figs. 1 and 2).

The time of day for laying accordingly varied with the season and locality. Obs. 1 to 7 were conducted in February and March, during the cool season, when the air temperature at the sites during laying seldom exceeded 85° F. Under these conditions, laying began at a late hour in the morning (11.00 hr., A.T. 77° F., Obs. 2) and was apparently not interrupted at midday. Obs. 9 was made in May and mass laying began much earlier (08.00 hr.) but at a similar air temperature (78° F.); it was interrupted at midday, when the air temperature rose to 92° F., and was resumed in the afternoon when the sky became overcast and solar radiation presumably decreased considerably although the air temperature did not. Obs. 10 was also conducted in late spring, but in cooler conditions (because of greater altitude), and laying again took place in the middle of the day within an air temperature range of 72–81° F.

The temperature requirements for laying activity were further emphasised on occasions by the position of the laying sites and the orientation of laying locusts in relation to insolation. This was best seen in Obs. 1. The site here consisted of an undulating, hummocky gravel plain intersected by minor runnels. All laying groups were on the slopes facing the sun and the individual locusts within them were orientated at right angles to the sun (Plate II, figs. 1 and 2, and Plate III, fig. 1).

3. THE SETTLING OF SWARMS IN RELATION TO LAYING SITES.

The available observations indicate that the settling of a swarm in an area in which a portion of it subsequently lays is not related to the suitability of the particular site for laying. It appears that mixed and perhaps also fully mature swarms, like immature migrant swarms, settle under the influence of such factors as fatigue and the visual attraction of the vegetation (Gunn *et al.*, 1948; Kennedy, 1951; Waloff and Rainey, 1951).

This is borne out by Obs. 2 and 9. In the former, the swarm alighted on the trees at dusk and did not descend to the ground until the following morning. In Obs. 9, some of the locusts alighted on the ground on arrival, but it is unlikely that they could have been attracted by the suitability of the site for laying, since the ground where they settled and the areas where laying subsequently took place were effectively covered by a layer of gravel (Plate IV, fig. 2) and the soft soil underneath could only be detected by probing, and this was not observed until 38 hours after the arrival of the swarm.

A further example can be given from an earlier observation in Iran. A mature swarm settled on 20th April, 1945, in the vicinity of Lingeh at a site which was quite dry and where the soil was hard. Attempts to oviposit in the soil were abortive and the eggs were scattered on the surface of the ground and on the vegetation, giving a yellowish tinge visible at some distance. Yet, at the same time, other swarms only 5–10 miles away were successfully laying in localities where conditions were more suitable.

A swarm may, however, be occasionally attracted to a suitable laying site by the presence of laying locusts. This was recorded during the second part of Obs. 1, from 16.00 to 16.30 hr., when numerous locusts differing in degree of maturity settled on a site occupied by groups of others that were already laying. Whether the presence of the laying groups was a decisive factor, or whether the swarm would have settled here in any case, is, of course, unknown; it is suggestive that a similar flight of locusts passed at 10.30 hr. without stopping.

4. SELECTION OF LAYING SITES.

The conditions and aspects of localities where egg-laying has been recorded differ very considerably. First impressions indicate that relatively little selectivity was involved in it since it occurred in areas differing as widely as a

TABLE III.—*Soil composition and moisture of egg-sites.*

Obs. no.	Date.	Soil composition.		Moisture below surface.		Remarks.
		General area.	Egg-site.	General area.	Egg-site.	
1	22.ii.51	Plain of silt and gravel; minor sandy water courses.	Slopes and banks of water courses; hummocks under vegetation. Soft alluvial sand partly covered by gravel and stones	?	1–2″	Laying in progress.
2	24.ii.51	As above	Hummocks at the base of vegetation and banks of water courses. Soft alluvial sand	Depth greater than at egg-site	1″	Ditto.
3*	26.ii.51	Undulating sandy plain	Shallow hollows. Homogeneous sandy soil	4″	2″	Ditto.
5	25.ii.51	As above, but with minor water courses	Bank of water course. Light sandy silt	3–4″ or greater	1″	Laying on about 18.ii.51.
6	8.iii.51	Gravelly and stony hillslope cut by runnels	Sandy bed of runnel in the lee of an overhanging rock	4″	2″	Hatching about to begin.
7	25.iii.51	Alluvial plain intersected by sandy runnels	Sandy beds of runnels	?	?	Laying in progress.
8	10.iv.51	Rocky gully	Soft soil in very small pockets between rocks	?	?	Hatching in progress.
9	24.v.51	Flat gravel plain with soft silty subsoil	Not visibly different from the general area	3–4″	3–4″	Laying in progress.
10	31.v.51	Undulating sandy, silty or gravelly valley	Sandy stretches	Moist to the surface, frequent showers		Laying in progress.

* This swarm was originally found on 25.ii.51, half-a-mile from this locality, where the soil was drier.

sandy plain (Plate V, fig. 1), on the one hand, and a stony slope (Plate II, figs. 1 and 2) and even a rocky gully (Plate III, fig. 2), on the other. Detailed examination of the laying areas, however, revealed that a considerable degree of selectivity is, in fact, shown by females in choosing the actual laying sites. A comparison between the egg-sites and the adjoining area is made in Table III which shows selection of egg-sites on all occasions except in Obs. 9, where the conditions were so uniform that selection was not obvious. It further suggests that selection was primarily governed by the composition and moisture content of the soil, and to some extent by temperature conditions.

In the cases listed in Table III, the moisture content of the soil at the egg-sites varied from completely moist (but not waterlogged) soil (Obs. 10) to drier soil, where moisture was encountered at a depth of 3–4 in. from the surface (Obs. 9). In the general semi-arid conditions that prevailed when these observations were made, selection was largely in favour of the dampest site; in all cases where the moisture of the soil was examined it was greatest at the egg-site, except in Obs. 9, in which the moisture conditions were uniform.

Dry soils were evidently avoided. In Obs. 3, a swarm of mature locusts was found copulating at 11.00 hr. on a sandy plain. They were scattered about without forming concentrations and none was attempting to lay. At 16.00 hr., the couples were still rather scattered, though some had formed loose basking groups. A few females were probing the ground, but again none was seen actually laying. On the following day, at 11.30 hr., the swarm was found half-a-mile east of the original locality, in an area which did not differ in general appearance from the original one. This displacement appears to have been achieved entirely by crawling, judging from the tracks left on the surface of the soil and from reports of the local shepherds, who had seen this swarm during the interval. About half the locusts were collecting in the shallow depressions and laying, while the rest were scattered about in couples. In the depressions where egg-laying was taking place, moisture was found at two inches below the surface. Examination of the locality where the locusts were found on the previous day failed to disclose any laying and indicated that the soil was dry to a depth of over four inches. This difference was the only apparent reason for the displacement of the population.

The type of soil chosen for oviposition consisted principally of soft sands and silts (Table III), which varied in their distribution and frequency of occurrence in the different areas. In Obs. 2 and 6, such soils were encountered in limited patches as hummocks under the vegetation, or along the beds of minor runnels (Plate III, fig. 1); in Obs. 8, they were confined to minute pockets in the spaces between rocks and boulders (Plate IV, fig. 1); in Obs. 9 and (partly) 1, the soft soils were concealed by a layer of gravel and stones (Plate II, fig. 1 and Plate IV, fig. 1); while in other observed cases, the sandy areas were more or less extensive (Plate V, fig. 1).

The selection of laying sites began in the crawling that took place during mating. In the initial stages of Obs. 1, 2, 3 and 9, the couples were evenly scattered over the site occupied by the swarm. Gradually crawling began, at first randomly, but later developing into a more co-ordinated movement, rather similar to that of a marching band of hoppers. This did not always involve the whole swarm, and some pairs proceeded in different directions. Marching tended to follow the line of least resistance and thus became canalised along runnels and depressions. If a pair stopped, the following pair often stopped also, and others in the vicinity did the same so that the pairs gradually aggregated. This sequence is shown in a series of photographs taken during Obs. 1. Plate I, fig. 1, shows scattered couples; those in the foreground are approaching the base of a hummock, others in the middle-distance are scattered randomly, and more can be seen in the background following the bed of a runnel. Plate I, fig. 2, shows the next stage, where couples have come to rest under a hummock and are being joined by others. Plate III, fig. 1, referring to Obs. 2, shows a similar stage; couples in the foreground are marching along a runnel, while initial concentrations can be seen under the hummocks on the opposite side of it, to the left and right of the standing figure. These concentrations are on the sunny side of the hummocks.

Sometimes concentrations of pairs formed at sites which afforded optimum conditions for basking or perhaps the highest humidity without being particularly suitable for laying. This was suggested by Obs. 4, where a concentration of mating adults was found on a heap of dry dung, left by generations of sheep and goats at this particular camping ground. The black dung must have differed from the surrounding whitish clayey plain in surface temperature due to insolation, and having preserved the moisture of the soil underneath, may have also offered more favourable humidity conditions. In any case, it proved more attractive to the mating locusts than the surrounding plain, although it is most unlikely that the females could penetrate the layer of dung pellets several inches deep, in order to lay in the soil below.

The final selection of sites was made by probing prior to laying. In Obs. 1, 2 and 9, during the halts made by the crawling pairs, females were occasionally seen probing the ground with their ovipositors. Not infrequently the probing was abandoned, but was resumed later after the pair had crawled some distance.

Pairs which commenced laying were joined by others in the vicinity and gradually large numbers collected together to form laying groups. Sometimes when conditions suitable for laying were lacking, as in Obs. 3, considerable displacement by crawling occurred. On the other hand, in some cases, as in Obs. 9, or in Obs. 2, laying took place at the first halt of the crawling pairs.

The course of events that leads to oviposition may be summarised as follows :

1. Random settling of swarm.
2. Pairing.
3. Initial selection of suitable conditions of temperature (and perhaps humidity) by crawling couples.
4. Final selection of laying sites by probing females.

5. Group Laying.

Noteworthy characteristics of the egg-laying groups were their isolation from one another, their compactness and the high density of the locusts in them. Examples of the distribution of these groups may be seen in fig. 3, Plate II, fig. 1, and Plate III, fig. 1. The behaviour of the crawling pairs leading to the formation of these groups suggests that visual gregarious attraction is involved to some extent. This is further borne out by the fact that the more open the site, the fewer and larger are the groups, as in Obs. 9, where there was least obstruction to movement and vision. Conversely, the more broken the terrain, the more numerous and the smaller are the groups ; this is particularly well shown in Obs. 2, where separate groups began to form under each individual hummock.

An example of the density of the locusts in a laying group is obtained from Plate II, fig. 2, which is a close-up of a section of the larger group in Plate II, fig. 1. The density of the egg-pods in this particular section was found to be 58 per square foot. The density at which pods were laid by one of the groups in Obs. 9 can be seen from Plate V, fig. 2 ; 82 pods were counted on the spade shown, giving a density of about 150 pods per square foot. The average number of eggs per pod on this occasion was found to be 100 ; on successful hatching this would have produced a density of the order of 15,000 hoppers per square foot. It is possible, however, that this site had been used more than once.

Such high densities could hardly be attained as a result of responses to environmental conditions alone, and the gregarious inter-attraction of locusts must have played the major part. Gregariousness is a factor which binds the locusts together through all stages of their lives, and similar high concentrations are encountered in basking and roosting groups of hoppers and adults.

However, the high degree of selectivity shown by locusts during laying may serve as a factor in concentrating them even when there is no gregarious tendency. This may be particularly important in heterogeneous areas, where the most acceptable complex of soil, humidity and temperature conditions occurs only in limited areas. Non-gregarious individuals may also be drawn together for laying in such circumstances, and this may initiate the aggregation of the next generation.

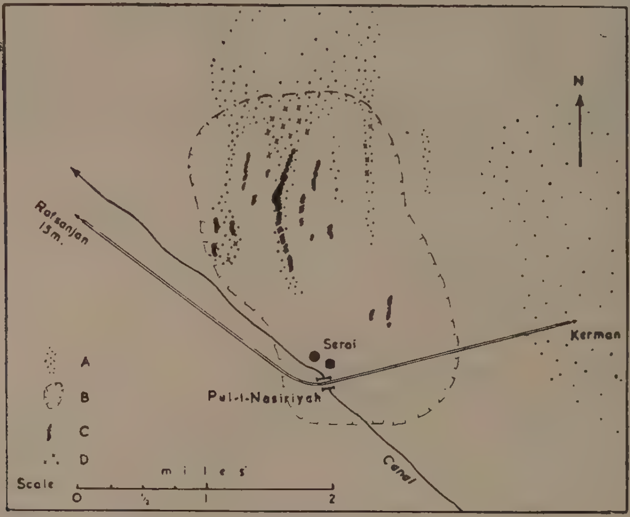

Fig. 3.—Obs. 9. Position of laying locust groups on the morning of 24.v.51. A. Shallow depressions with finer gravel and denser vegetation than on the adjoining plain. B. Approximate position occupied by the swarm on its arrival, on the afternoon of 22.v.51. C. Dense groups of mainly laying locusts at 08.30 hr. on 24.v.51. D. Scattered loose groups of mainly immature adults on the same morning.

SUMMARY.

Swarms of the Desert Locust (*Schistocerca gregaria* Forsk.) observed during the 1950–51 winter-spring season in southern Iran varied in the proportion of mature and immature individuals and in sex-ratio. Differential behaviour of mature and immature locusts explains this variation, the mature individuals tending to remain at a roosting site when the immature ones depart, and the sexes differing in rate of maturation and therefore in behaviour.

Mating commenced at an air temperature of 64° F. and coincided in time with the start of the vigorous flying activity of the immature locusts of the same swarms. It was sometimes accompanied by other forms of activity.

Mass oviposition was recorded within an air temperature range of 72° to 92° F., but the preliminary probing sometimes began at lower temperatures.

The settling of a mixed swarm in an area in which the mature females in it subsequently laid seemed to be attributable, like that of immature migrant swarms, to such factors as fatigue and visual attraction of vegetation, and to be unrelated to the suitability of the area for laying. After settling, the initial selection of egg-laying sites was made by copulating pairs while crawling, and the final choice was made by the probing of females. The selection of sites was apparently governed by a preference for certain moisture, soil and temperature conditions.

Females ready to lay assembled in groups characterised by isolation and compactness and by the high density of locusts within them. It is suggested that the position and size of the groups were related to the nature of the terrain, but there appeared to be no reason for the high density other than gregarious inter-attraction.

The high degree of selectivity shown by locusts in their choice of laying sites may be important as a factor in the concentration of non-gregarious individuals.

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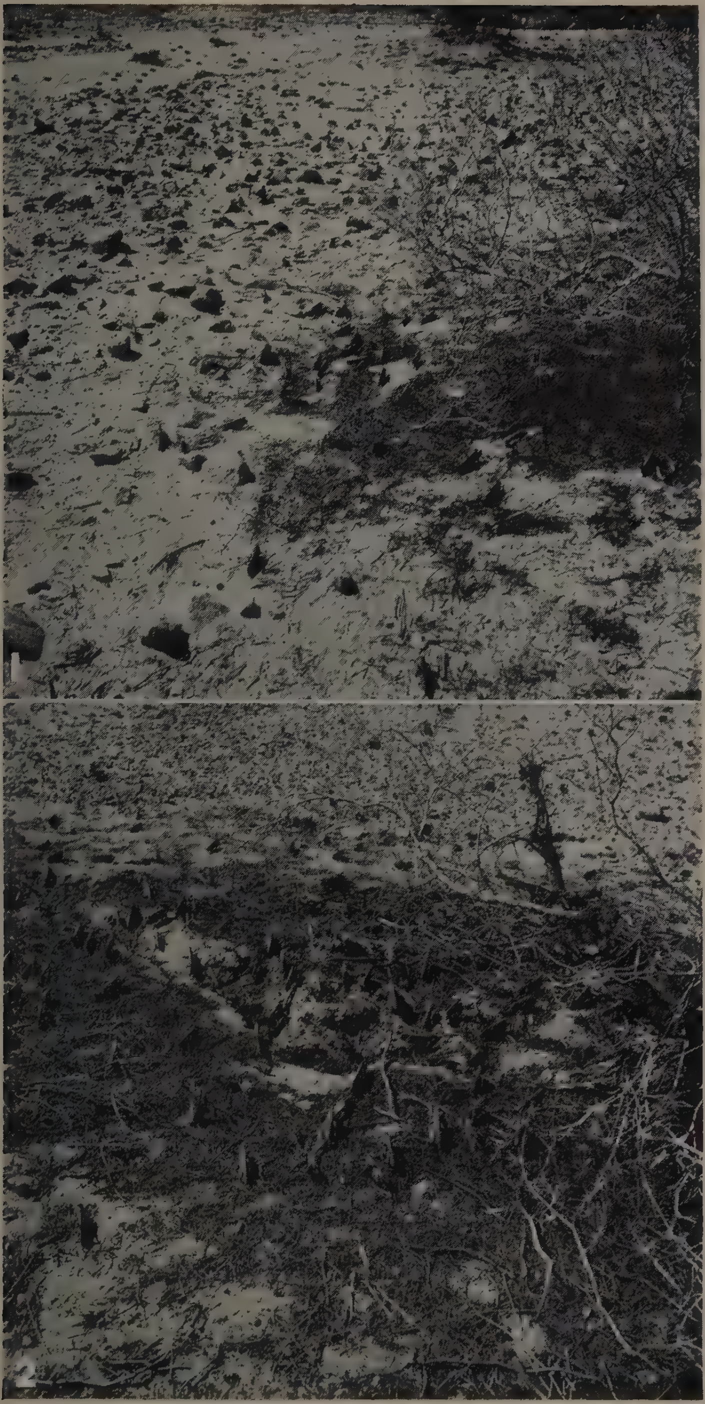
PLATE I.

Fig. 1.—Obs. 1. 10.30 hr.; mating locusts dispersed on the ground.

Fig. 2.—Obs. 1. 11.00 hr.; couples beginning to concentrate into loose groups.



The behaviour of swarms of the Desert Locust during oviposition in Iran.

G. B. Popov.

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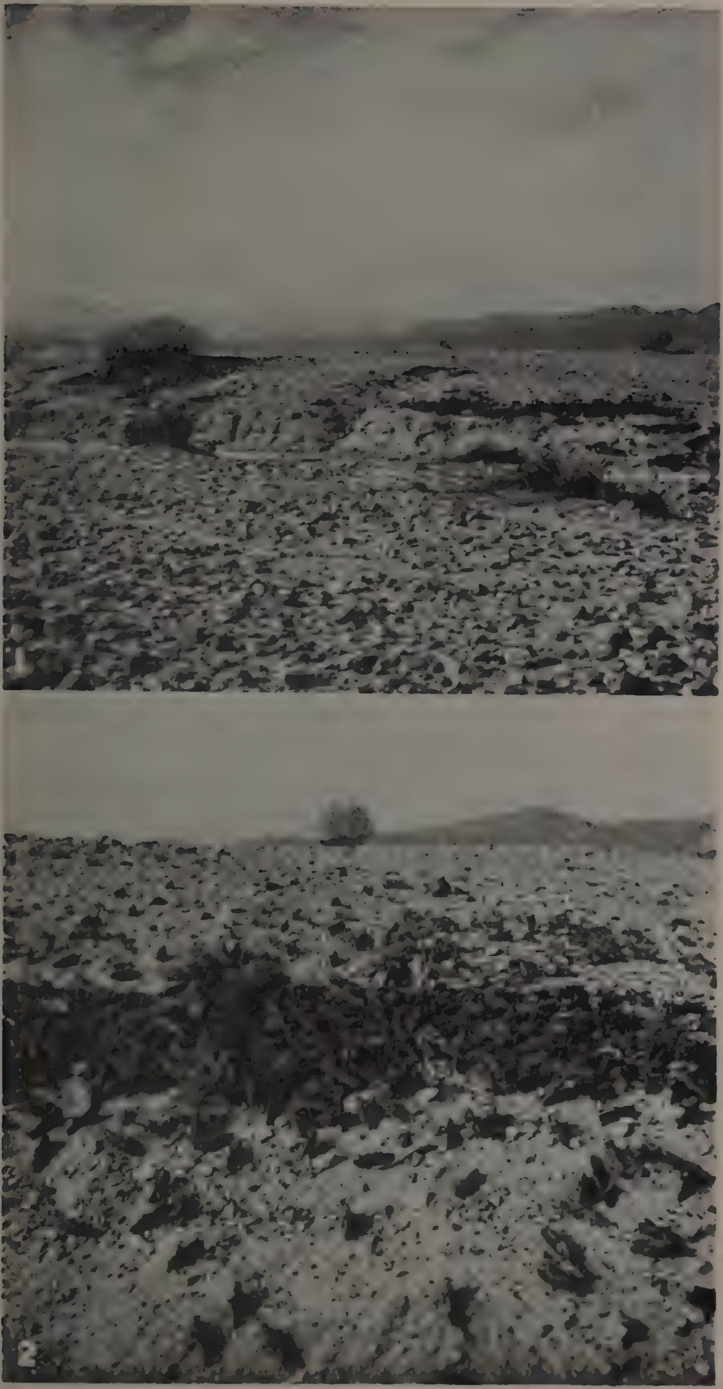
PLATE II.

Fig. 1.—Obs. 1. 15.45 hr.; locusts laying in compact groups.

Fig. 2.—Obs. 1. Closer view of one of the laying groups in fig. 1.



The behaviour of swarms of the Desert Locust during oviposition in Iran.

G. B. Popov.

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PLATE III.

FIG. 1.—Obs. 2. Scattered mating pairs beginning to collect into loose groups along sandy runnels dissecting a gravelly slope.

FIG. 2.—Obs. 8. An egg-site in a rocky gully. Arrow indicates position of an emergence hole. (Further detail shown in Plate IV, fig. 1.)

PLATE III.

The behaviour of swarms of the Desert Locust during oviposition in Iran.

G. B. Popov.

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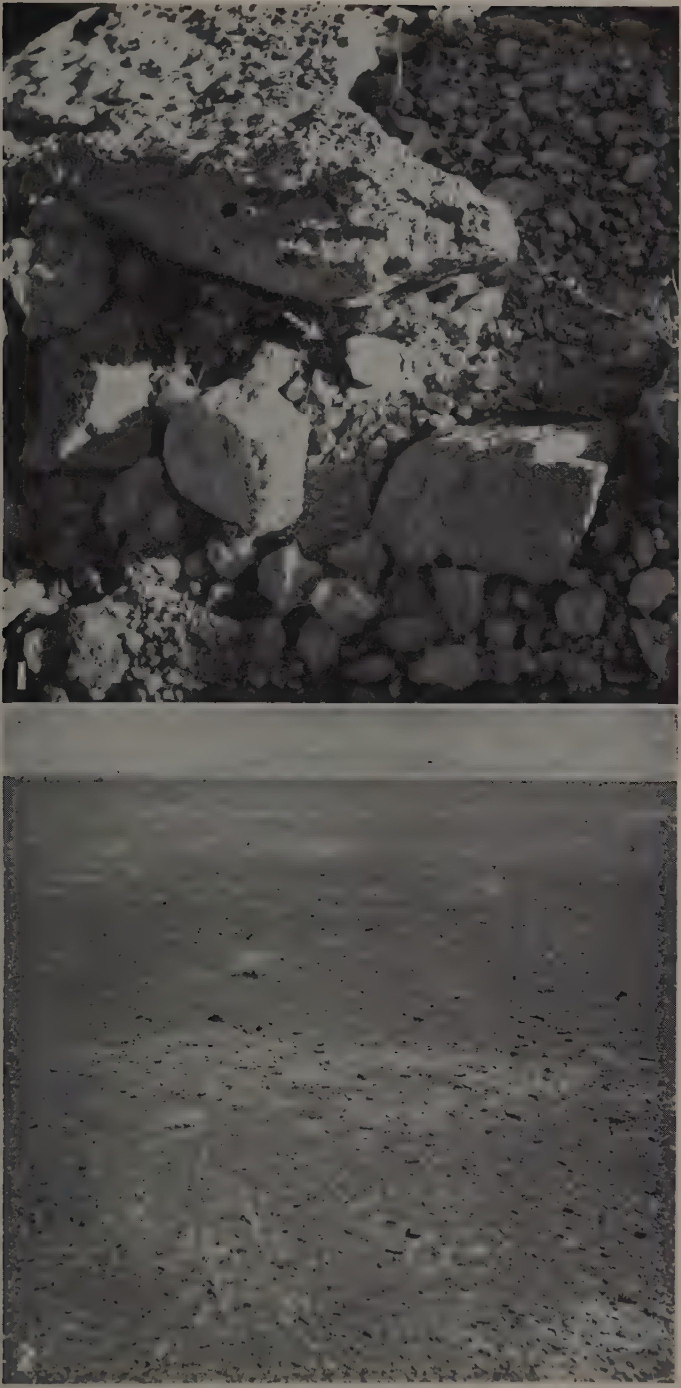
PLATE IV.

Fig. 1.—Detail of Plate III, fig. 2; the arrow indicates one of the emergence holes.

Fig. 2.—Obs. 9. An egg-site recognisable by its whitish appearance which is due to silty sub-soil showing through gravel disturbed during laying.



The behaviour of swarms of the Desert Locust during oviposition in Iran.

G. B. Popov.

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PLATE V.

FIG. 1.—Obs. 10. An egg-laying area on an undulating sandy plain with scattered, low-growing bushes.

FIG. 2.—Obs. 9. A sample of egg-pods from a very dense laying site.

PLATE V.

The behaviour of swarms of the Desert Locust during oviposition in Iran.

G. B. Popov.

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STUDIES ON THE BIOLOGY AND ECOLOGY OF THE GALL-PRODUCING APHIDS OF THE TRIBE FORDINI (HOMOPTERA: APHIDOIDEA) IN ISRAEL.

By Guta Wertheim.

(*Department of Entomology, The Hebrew University, Jerusalem, Israel.*)

Communicated by Mr. J. P. Doncaster.

Manuscript received 26th September, 1953.

(Read 4th November, 1953.)

With 1 Plate and 8 Text-figures.

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I. Introduction.

The tribe Fordini comprises a group of species producing galls on *Pistacia.* In Israel three species of *Pistacia* are attacked: *P. palaestina* Boiss., *P. atlantica* Desf. and *P. lentiscus* L. On *P. palaestina* five species occur: *Baizongia pistaciae* L., *Geoica utricularia* Passerini, *Forda semilunarius* Passerini, *F. follicularia* Passerini and *Paracletus pallidus* Derbès. On *P. atlantica*, four species occur: *Geoica utricularia*, *Forda derbesi* Lich., *F. riccobonii* Stefani and *Aploneura* sp. Only one species, *Aploneura lentisci*, was found on *P. lentiscus.* (Bodenheimer, 1927.)

The biology of these insects was described nearly a century ago by Derbès (1869) and Courchet (1878) in Southern France. The main facts of the complex life cycle may be summarised as follows: The fundatrix hatches from an overwintering egg in the spring. It starts sucking on young leaves and as a result a gall is formed. During the spring, summer and early autumn the fundatrix and her offspring develop within the gall. In the fall the gall opens and a winged generation leaves it. Development is continued on Gramineae roots, where, towards the spring, a new generation of winged forms, the sexuparae, develops. These return to the *Pistacia* tree and give birth to the sexuales. The male dies after mating and a single egg develops in the female. The female dies retaining the unlaid egg, which remains for a year on the bark and hatches next spring.

The cycle is thus biennial and comprises generations developing on two host-plants and a resting stage in the form of an overwintering egg (fig. 1).

Very little was known of the biology of these insects in Israel and it was the author's aim to investigate their life cycle, the development of the galls and their insect population and the manner of migration from the *Pistacia* tree to the Gramineae roots.

II. Materials and Methods.

All field observations were carried out in the Hebrew University Botanical Garden on Mount Scopus, where a large number of *P. palaestina* trees and *P. lentiscus* shrubs was cultivated. The galls on *P. atlantica* were investigated on a single tree in Jerusalem. Young shoots on which fundatrices appeared were marked with coloured cloth ribbons to ensure their visibility amid the developing dense foliage. At the beginning of the season, observations of the fundatrices and young galls were made at least once daily. When the galls assumed their definitive shape, measurements were taken approximately once a fortnight. The length of the galls was determined by spanning a thread from the tip to their point of attachment to the leaf or branch; their diameter, at the widest point, was measured with a nonius. Thus the growth of the galls could be followed directly on the tree. Population counts of the insects contained in picked galls were carried out. In densely populated galls the injection of a few drops of ether facilitated the count and prevented the dispersal of the insects. Experiments on the flight of winged aphids were carried out in a wooden box 100 × 80 × 60 cm. provided with a movable wall which could be replaced by a glass window or a black cloth to create conditions of full light or darkness. A dish of ice cubes or an electric bulb of 100 w. covered with black cloth were introduced into the box to induce temperature changes as desired.

In experiments on longevity of the winged forms and their offspring under constant temperature and constant relative humidity the usual series of changing concentrations of sulphuric acid was used. For 0 per cent. and 100 per cent. R.H. phosphorus pentoxide and distilled water were employed. The solutions were kept in test tubes into which a length of narrow glass tubing was inserted; small plugs of cotton wool covered with black cloth were placed in the centre of these tubes and the insects were kept on them.

III. The Gall, its Development and Content.

The galls occurring on *Pistacia* can be divided into two types: (*a*) Hollow, bag-like structures entirely closed off from the outside, opening in the fall

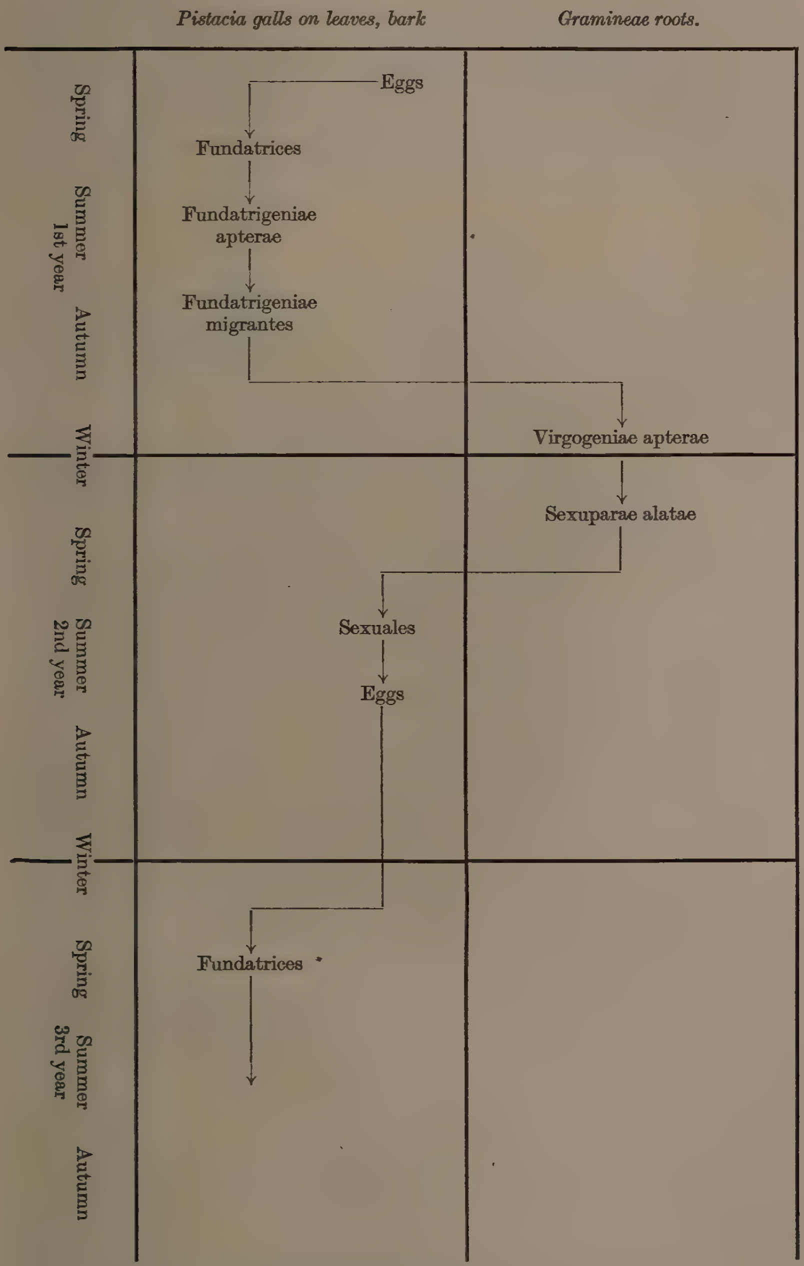

Pistacia galls on leaves, bark
Gramineae roots.
Spring
Summer
1st year
Autumn
Winter
Spring
Summer
2nd year
Autumn
Winter
Spring
Summer
3rd year
Autumn
Eggs
Fundatrices
Fundatrigeniae apterae
Fundatrigeniae migrantes
Virgogeniae apterae
Sexuparae alatae
Sexuales
Eggs
Fundatrices

Fig. 1.—Schematic summary of the life-cycle of the Fordini.

due to the splitting of their wall. To this type belong the galls produced by *B. pistaciae*, *G. utricularia* and *Aploneura* sp. (*b*) Pocket-like structures produced by the upward folding of the edge of the leaflet and its approximation to the surface of the leaflet. Thus a gall is formed whose folded margin may nevertheless nearly be open. Such a gall opens when the folded part of the leaflet detaches itself from the blade. To this type belong the galls produced by species of *Forda*, *Paracletus pallidus* and *Aploneura lentisci*.

(a) *Bag-like galls.*

Baizongia pistaciae.—The gall produced by this aphid is an elongated, cylindrical, horn-like structure (Plate I, fig. 1.); it is crimson at the beginning of development, turns green during summer, and yellowish green towards the end of the season.

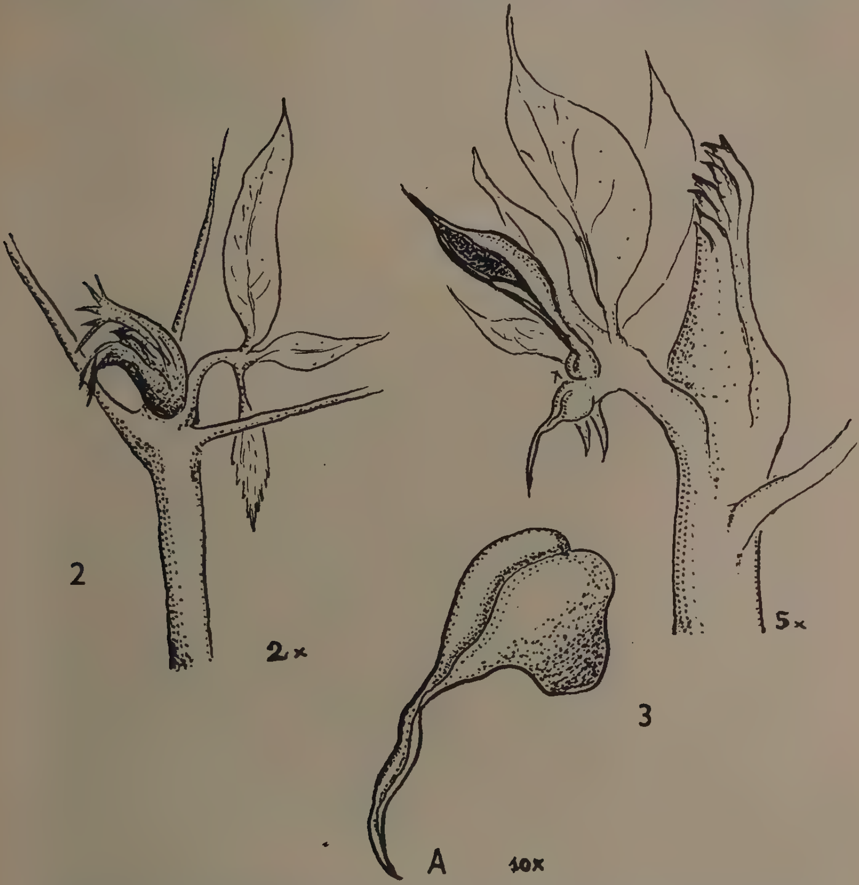
Since fully grown galls appear attached to the branch, they were believed to be produced by a change in form of the entire compound leaf. But, as already observed by Roberti (1939) and described in detail below, each gall is formed on a single leaflet.

The newly hatched fundatrices appear on the young shoots from the end of March till the middle of April. Hatching is not simultaneous, and free insects and young galls can be observed at the same time. The fundatrix begins to suck at the base of the smallest embryonic compound leaf at the apex of a shoot. Several insects may be observed around each shoot tip and accordingly several galls may develop on one compound leaf. The first visible reaction of the plant tissue is observed 6 to 8 days after the insect begins to suck. The stem of the shoot, or sometimes only the leaf petiole, bends, forming an angle of 60° to 90° with the branch (Plate I, fig. 1). The insect then changes its place, probably under the influence of changes in turgor of the host tissues, and settles on a leaflet. The latter, still in the embryonic state, is folded longitudinally, both edges of the blade being rolled inwards towards the main vein. Thus the insect is now enclosed by the folded parts of the leaflet on the surface of which a single crimson spot can be observed (fig. 3). A small, hollow outgrowth on the underside of the leaflet is now formed, while the edge of the attacked leaflet closes over the insect by uniting with the main vein as a result of active growth. Thus the insect becomes enclosed in a small triangular gall (fig. 4). The whole process lasts from 14 to 16 days: 6–8 days till the bending of the leaf and about 7 days from the time the insect settles on the leaflet till the gall closes. Concurrently changes appear in the entire compound leaf. The petiole ceases to elongate and becomes thicker. For a certain additional period the remaining unattacked leaflets continue to develop, but during the summer they desiccate, and the thickened petiole, which is not more than 10 to 15 mm. long (as compared with 100 to 110 mm. in the normal compound leaf) becomes brown, and the gall then appears to be a direct outgrowth of the branch.

The mature galls vary greatly in size and no two of identical proportions can be found on a single tree. Galls attaining over 250 mm. in length were observed together with small ones 20 to 30 mm. long, which nevertheless contained normally developed populations (Plate I, fig. 1). Thus no attempt was made to compute statistical data on gall dimensions or their insect populations.

The measurements and insect counts merely refer to the general trend of growth and development.

In Table I population counts are computed. For each date indicated in the table several galls of approximately equal size were collected and their insect populations were counted. Each reference in the table corresponds to the population and dimensions of a single gall.



Figs. 2–3.—(2) Young shoot of *P. palaestina* bent under the influence of sucking of *B. pistaciae.* (3) Leaflet of *P. palaestina* enlarged at the base and containing the gall-causing aphid. A. Same leaflet enlarged.

As can be seen from Table I the gall is produced and attains its characteristic shape under the influence of the fundatrix alone. Further growth is stimulated by the developing fundatrigeniae. If, as occasionally happens, the stem mother dies before giving birth to her offspring, the growth of the gall is arrested.

TABLE I.—Baizongia pistaciae : *number of aphids and dimensions of the galls (in mm.) during development.*

				Wingless aphids.				Winged aphids.			
Date (1945).	Length of gall.	Width of gall.	Fundatrix.	1 and 2 inst.	3 inst.	4 inst.	Adults.	Young nymphs.	Nymphs with wing buds 3, 4 and 5 inst.	Adults.	Total.
8·v	4.0	2.0	2 inst.	.	.	.	.	.	.	.	.
15·v	8·2	3·7	2 ,,	.	.	.	.	.	.	.	.
	19·0	3·8	3 ,,	.	.	.	.	.	.	.	.
20·v	10·4	4·0	4 ,,	.	.	.	.	.	.	.	.
23·v	24·0	4·3	Adult	2	.	.	.	.	.	.	3
30·v	35·3	3·8	,,	5	.	.	.	.	.	.	6
8·vi	26·6	2·8	,,	3	1	.	.	.	.	.	5
27·vi	40·2	3·8	,,	19	4	1	2	.	.	.	27
	55·4	5·2	,,	22	7	1	2	.	.	.	33
6·vii	51·3	4·8	,,	56	2	3	12	.	.	.	74
9·vii	72·4	7·3	,,	106	55	12	20	.	.	.	194
15·vii	62·3	6·8	,,	63	12	4	4	.	.	.	84
26·viii	94·0	10·3	Dead	446	149	118	31	.	.	.	745
7·ix	115·0	25·0	,,	141	65	38	308	2,419	.	.	2,972
6·x	147·0	37·0	,,	.	.	.	483	148	3,208	.	3,840
15·x	150·0	28·0	,,	.	.	.	549	9,623	.	.	10,173
3·xi	220·0	20·0	.	.	.	.	658	.	.	7,215	7,874

One day after the final moult the fundatrix commences to produce offspring. These (12 to 20 in number) are wingless forms, which in turn produce a second generation of wingless aphids. Only the third filial generation, which appears toward the end of August, develops into winged insects.

The galls open during the period from the end of October through November. At the side of the opening, which is as a rule near the tip of the cylindrical gall, appear small droplets of resin, characteristic of the *Pistacia* tree. Splits then appear at one point. The edges of the split turn outwards, thus forming a wide opening. Each gall opens at only a single point, through which the winged aphids leave, while the wingless forms remain in the gall until its wall dries up and blackens. Living, wingless insects were occasionally found in dry galls as late as January. After the reproduction period is over the ovoid bodies of the wingless aphids which were formerly yellowish, become deeply orange and shrink considerably. Thus old wingless forms may readily be distinguished by their colour and shrunken, spherical bodies from other forms within the same gall. Only old forms are later found in dry empty galls.

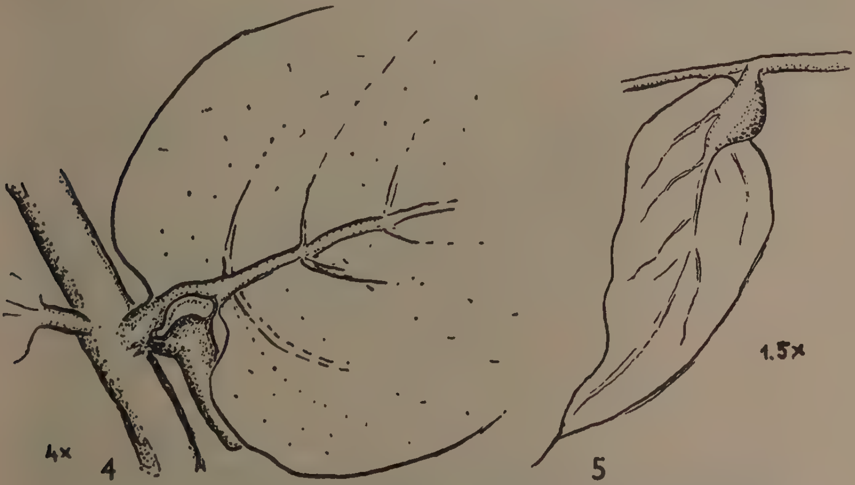
Except for the fundatrix, which is usually found dead in August, no dead aphids were observed in normal galls, which were not attacked by predators or parasites of the aphids.

Since the galls of *B. pistaciae* are connected directly to the branch, they are not shed when the leaves fall in the autumn. Black, dry, empty galls from previous years may be observed on the trees throughout the year.

Geoica utricularia Passerini.—The irregularly spherical, yellowish-pink gall produced as a result of the sucking of this aphid was reported by Houard

(1908) from four species of *Pistacia : terebinthus*, *lentiscus*, *vera* and *mutica*. Roberti (1939) described it as being formed on the underside of the leaflet blade. Neither of these observations was confirmed. Among all the galls produced on the three species of *Pistacia* in Israel that of *G. utricularia* is the only one occurring on two species of host plant : *P. palaestina* and *P. atlantica*. The galls on the two trees differ in colour and in the character of their walls. Those on *P. atlantica* are green, more irregular in shape and their external wall is wrinkled and uneven ; while those on *P. palaestina* are yellowish pink, have smooth surfaces and a more regularly spherical shape.

The newly hatched fundatrix can be observed in April on young leaflets, near the base of the blade, close to the main vein. After about two days of sucking, the tissue around and beneath the insect thickens, the vein in the vicinity of the insect becomes coarser and purple in colour while the edge the the attacked leaflet becomes undulating, and a part of its surface closes over the insect as a result of active growth (fig. 5). The gall at first consists of a solid mass of tissue with 2 to 3 small cavities corresponding to the distances between the side veins of the leaflet blade. In one of these cavities the fundatrix is found. Occasionally two fundatrices can be found in one young gall. In this case one dies before the first moult, so that only a single female continues to develop. As the gall grows it becomes spherical, its wall becomes thinner and the ripe gall consists of a hollow structure with a wall thicker than the leaf blade.



Figs. 4–5.—(4) Young gall of *B. pistaciae*. (5) Early stage in development of the gall of *G. utricularia*.

As in the case of *B. pistaciae* the fundatrix alone provokes gall formation and growth during the first month. In galls which are 5 to 8 mm. long, only the fundatrix is found. The insect starts to reproduce the day after the fourth moult. It gives birth to about 20 wingless aphids. The first generation of fundatrigeniae attains maturity in 30 to 35 days and in turn begins to reproduce. The total number of adult wingless insects in the gall does not exceed 100, while the number of first instar larvae in August is much greater. This indicates that of the offspring of the first generation some develop into wingless forms of the second generation and some into winged forms. The second generation of wingless aphids also produces winged offspring.

The galls start to open at the end of September and continue until the middle of October. Only a few remaining galls open at the end of October. Droplets of resin appear on the gall and subsequently the wall splits in all directions from one point, thus producing a wide opening through which the winged aphids leave. The wingless insects remain in the open gall till it dries up and falls from the tree during leaf-fall in November.

Aploneura sp.—The gall induced by this aphid differs from all other species in its course of development, in the biology of its inhabitants and in its phenology (Table IV). While all other *Pistacia* galls develop on leaves, this species attacks the resting buds. At first an elongated, green, cylindrical outgrowth is produced. Additional cylinders are added to the basal one by growth and branching, until finally a bizarre-shaped gall is produced (Plate I, fig. 2). The gall, green at the beginning of its development, turns crimson towards the end of the season and opens in September by means of numerous splits, one at the tip of each branch. Contrary to the previously described cases, where the winged insects give birth to parthenogenetic offspring, in this species the winged aphids that leave the gall are the sexuparae. In the laboratory they give birth to males and females. Their fate in nature requires further investigation.

(b) *Pocket galls.*

Paracletus pallidus and all species of *Forda* differ in their life histories and in their method of gall formation from the previously described species. Only *Aploneura lentisci*, although forming a pocket-shaped gall, develops like the aphids which form bag-shaped galls.

The fundatrix of the above-mentioned genera hatches in early spring towards the middle of March, usually even before the opening of the buds. Newly hatched larvae can be observed in crevices on the twigs. As soon as the buds open, the fundatrices settle on the small embryonic leaflets between the halves of their blades which are rolled towards the main vein, where they commence sucking. A crimson spot appears at the point of puncture and a small pea-shaped gall is formed. When the leaflet blade flattens out during development two small areas remain adherent, enclosing the insect and usually a part of the main vein. Thus the crimson gall, no larger than a pea, protrudes on the under side of the leaflet, with its opening on the upper side (fig. 6). The juxtaposed edges of the gall remain separated by a narrow slit so that the gall actually always remains open.

These galls, first observed by Derbès (1869), were called by him temporary galls, as only the fundatrices develop in them. They are produced by the stem mothers of all pocket-gall producing species and are all alike in colour, form and size. From the temporary gall alone, the species cannot be determined.

In the temporary gall the fundatrix attains maturity after four moults and starts to give birth to larvae, which leave the gall a few hours after being born.

These first instar fundatrigeniae settle on adjacent young leaflets and produce permanent pocket galls characteristic for each species. Thus the final galls are produced not by the stem mothers but by the first filial generation of wingless aphids. After the period of reproduction is over, the fundatrix dies in the temporary gall which persists on the tree until leaf-fall in autumn.

As may be seen in Table II for *F. derbesi*, two generations develop in the final gall : a wingless one, 5 to 14 in number, and their offspring consisting of winged forms, the second and the third fundatrigeniae respectively.

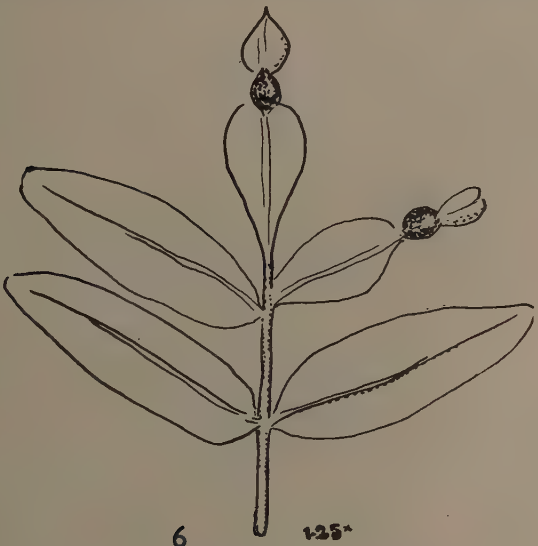


Fig. 6.—Temporary galls on *P. atlantica*.

In Tables I and II the increase in number of aphids in a bag- and pocket-gall are presented in detail. In a similar manner all other galls were examined and the number of filial generations together with the number of insects observed per gall in each species are presented in Table III.

(c) *Phenology of galls in Jerusalem and vicinity.*

In Table IV phenological data on the dates of appearance and opening of the galls are shown.

(d) *Dedifferentiation of temporary galls.*

Attention was paid mainly to the biology of the aphids, and no attempt was made to investigate the anatomy and physiology of the gall or the nature of the morphogenetic stimuli leading to gall formation. However, an interesting phenomenon of dedifferentiation of galls already formed was observed and is described below.

Table II.—Forda derbesi : *increase in number of aphids in the gall during a single season.*

Date.	First fundatrigenia.	First generation (wingless).		Second generation (winged).			Total.
		Larvae.	Adults.	Young nymphs.	Nymphs with wing buds.	Adults.	
29·v	1	.	.	.	.	.	1
	1	.	.	.	.	.	1
	1	3	.	.	.	.	4
15·vi	Dead	6	.	.	.	.	7
22·vi	1	14	.	.	.	.	15
	Dead	11	.	.	.	.	12
	,,	6	.	.	.	.	7
18·vii	,,	9	.	.	.	.	10
21·viii	1	9	.	.	.	.	10
	1	9	.	.	.	.	10
	1	9	.	.	.	.	10
16·ix	1	.	5	.	.	.	6
	1	.	5	.	.	.	6
	1	.	6	13	.	.	20
28·ix	Dead	.	8	8	.	.	17
	,,	.	7	3	.	.	11
	,,	.	9	6	.	.	16
	,,	.	7	.	.	.	8
5·xi	,,	.	9	.	20	2	32

Table III.—*Number of generations of aphids and maximum number of insects counted for each species.*

Species.	Number of generations.	Maximum number of insects per gall.
B. pistaciae	3	10,173
G. utricularia	3	805
F. semilunarius . . .	2	210
F. follicularia	2	15
F. derbesi	2	32
F. riccobonii	2	116
P. pallidus	2	57
A. lentisci	2	153

Table IV.—*Phenological data on the dates of appearance and opening of the galls.*

Species.	Date of appearance of the galls.	Date of opening of first galls.	Date of emptying of last galls.
Temporary galls .	15·iii–30·iii	.	.
B. pistaciae . .	4·iv–24·iv	2·xi	18·xi
G. utricularia . .	10·iv–20·iv	26·ix	17·xi
F. semilunarius .	8·iv–17·iv	29·x	18·xi
F. follicularia . .	.	3·xi	12·xi
P. pallidus . .	10·iv	25·x	7·xi
A. lentisci . .	15·iv– 9·v	3·xi	18·xi
F. riccobonii . .	15·iv–20·iv	2·xi	9·xi
F. derbesi . .	10·iv–17·iv	2·xi	11·xi
Aploneura sp. . .	25·v–10·vi	15·ix	20·ix

Lewis and Walton (1947) expressed the opinion that gall formation is an irreversible process and that from the moment a gall starts to develop the affected plant tissue cannot return to its normal condition. This is contrary to Zweigelt's observation that plant tissue can return to normal when the stimulus leading to gall formation acts for a short period only (Zweigelt, 1930 : 485).

In the case of the temporary galls produced by species of *Forda* and *Paracletus*, complete dedifferentiation of fully grown galls was observed. As stated above, the temporary galls begin to develop on very young leaflets, often on the day of the opening of the buds. If the fundatrix finishes its laying period and dies or ceases to suck for any other reason, such as infestation with parasites, before the leaflet attains maturity, the gall opens along the edges uniting both halves of the leaflet ; two concave, crimson halves of the gall may still be observed close to the main rib on both sides ; gradually the colouration disappears, the concavities flatten out and the leaflet regains its normal colour and shape, while only a small patch of lighter green on its surface or a slight deformation indicates that a gall has once been formed and disappeared during the leaflet's development. In cases where the leaflet reaches maturity before the death of the fundatrix, no dedifferentiation occurs and the gall persists on the tree till autumn.

IV. THE ECOLOGY OF THE AUTUMN MIGRANTS AND THEIR FIRST INSTAR OFFSPRING.

Courchet (1878) was the first to observe that after the opening of the galls, the winged aphids migrate to roots of various Gramineae. In Israel, flight occurs at the end of a long dry season when Gramineae, either wild or cultivated, are not available. It was thus of interest to determine whither these insects migrated and what conditions influenced their flight.

The available data on the influence of humidity on the flight of aphids are controversial. Davies (1935) obtained a decrease in activity with a rise in relative humidity, while Broadbent (1949*a*) found that the aphids flew readily in humidities between 50 to 100 per cent. at a temperature below 26·7° C.

The influence of humidities prevailing at the time of the flight of *G. utricularia* was tested. The insects were maintained in large desiccators over sulphuric acid at concentrations providing 20, 40, 60 and 70 per cent. relative humidities, respectively. Under these conditions in diffuse light (more than 10 foot-candles) and at a temperature of 25 to 26° C. no differences could be observed in their readiness to fly. The insects took to wing almost immediately after the galls were opened, and the galls were emptied with the same speed in all relative humidities.

Temperature and light proved to be the main factors influencing flight. Table V presents the results of a typical experiment in which the aphids were kept in the dark. Two galls containing about 1500 aphids were used.

When the movable wall of the box was replaced by a sheet of white paper and weak diffuse light (approximately 6 to 8 foot-candles) was thus introduced, no flight could be observed under the same conditions of temperature and relative humidity as in Table V.

TABLE V.—G. utricularia : *behaviour of winged aphids in the dark.*

Time.	Temperature (°C.).	Per cent. relative humidity.	Behaviour of aphids.
8·55	15	58·5	No flight
9·30	15·5	57·0	,,
10·15	19·0	57·5	,,
10·45	20·5	57·0	,,
11·40	26·0	52·0	,,
12·40	28·0	50·0	,,
1·30	30·0	37·0	,,
2·30	31·0	35·0	A few aphids crawling on the wooden frame
3·30	30·0	34·0	No flight
4·30	33·0	30·5	,,

Light was thus indispensible for the flight of these insects. Under adequate illumination flight begins at 24 to 24·5° C.

Observations on winged aphids kept in cages together with their host-plant (seedlings of Gramineae) showed that they differ from winged forms of other species which have been studied extensively in connection with transmission of virus disease.

When seedlings of *Hordeum* or *Avena* grown in the laboratory, or cultivated *Poa* and *Cynodon* were offered to the aphids, the insects were not attracted by the plants; they flew to the glass windows, assembled there and laid their larvae directly on the glass or on the wooden frames. All young are born almost simultaneously, and the adults die soon afterwards without taking food in the period between their release from the gall until death. When kept separately in test tubes at room temperature, the aphids laid their larvae without any flight. The numbers of larvae produced under these conditions were :

G. utricularia.	*F. semilunarius.*	*B. pistaciae.*
5 to 8	5 to 7	5 to 8
Mean 7·63 ± 0·14	Mean 5·75 ± 0·25	Mean 6·73 ± 0·33

Tables VI and VII present data on the longevity and number of offspring of winged *G. utricularia* under controlled conditions.

TABLE VI.—G. utricularia : *longevity of winged fundatrigeniae in days.*

Temperature. (°C.).	Per cent. relative humidity.									
	0	10	20	40	60	70	80	90	100	
5 . .	18	18	22	24·5	26·5	31·2	35·2	30	30	$n = 12$
16 . .	3·7	5·3	4·7	5	6	6·6	3·4	9	4	$n = 16$
20 . .	2·8	3·7	3	3·7	3	4·7	8	7	3·1	$n = 16$
25 . .	1·7	1·9	2·5	1·2	3·5	5	6	5·6	6	$n = 16$
30 . .	1·5	1·5	2·2	2·5	3·2	3·1	3	3·3	3·8	$n = 16$
35 . .	1	1	1	1·2	1	1	1	1	1	$n = 16$

(n = number of aphids.)

Table VII.—G. utricularia : *mean number of larvae laid by one winged female.*

(Under extreme conditions of temperature and relative humidity most of the insects die without giving birth ; non-viable larvae are sometimes laid.)

Temperature (°C.).	Per cent. relative humidity.								
	0	10	20	40	60	70	80	90	100
5	0·2	0·7	0	0	0	0·6	0	0·6	0
16	6	6·7	6	3·1	4·6	3·3	2·6	4·3	0·6
20	6·2	6·2	3	5·7	6·5	5·5	2	3·2	3·2
25	6·5	6·5	7·2	5	4·5	4·7	3	4	1
30	5	6	4·5	5·5	3·5	5·2	6	2	5·5
35	.	.	0·25	1·2	.	.	.	.	.

In nature, flight from the open gall can be observed during all hours of daylight. The insects leave the gall 2 or 3 at a time ; when the gall is in direct sunlight all insects take to wing and the gall is emptied within 10 to 15 minutes. The flight is mainly in the direction of the wind. The insects thus disperse in all directions from the *Pistacia* tree.

Further indications as to the mode of transfer from the *Pistacia* trees were obtained by the study of the first instar larvae, offspring of the winged fundatrigeniae.

When born in vessels containing seedlings of Gramineae the young larvae immediately start sucking on the roots, especially on the parts close to the seed. But they can survive for long periods without any food at low temperature and high relative humidity. Tables VIII and IX deal with the average and maximum longevities of the first instar larvae under controlled conditions and without feeding. At a temperature of 16 to 20° C. and under 80 to 90 per cent. relative humidity the insects can survive up to 35 days. This period was markedly increased when the young larvae were kept in a greenhouse, in an earthenware vessel filled with wet sand and covered with a glass plate. The temperature changed from 14 to 15° C. by day to 3 to 4° C. at night. The humidity was high. Under these conditions a small percentage (1 to 2 per cent.) of larvae survived without feeding as long as 117 days, from November until April.

During this entire period the larvae remain in a semi-dormant state. However, this is not a true diapause, since they immediately start sucking as soon as they are offered germinating grass.

Migration from *Pistacia* to the roots of Gramineae can thus be assumed to occur as follows : the winged forms disperse in all directions from the tree and lay their offspring at random under stones or on the ground at the conclusion of their flight, probably towards evening. Only those young larvae which are laid in humid cool places survive until the rainy season and continue to develop when the seeds in their vicinity start to germinate. The mortality of those born in September and October is probably very high, but the survival of a small percentage of those born in November ensures further development in view of the enormous numbers of winged forms escaping from the galls each autumn.

TABLE VIII.—G. utricularia : *mean longevity of first instar larvae* (*days*).

°C.	5°.	16°.	20°.	25°.	30°.	35°.
0% R.H.	3 *n* = 1	7·26±0·4 *n* = 30	6·12±0·11 *n* = 65	3·99±0·13 *n* = 58	1·95±0·04 *n* = 58	
10	3 *n* = 3	12·75±0·8 *n* = 37	7·34±0·19 *n* = 59	3·68±0·09 *n* = 64	2·40±0·09 *n* = 52	
20	—	12·40±0·5 *n* = 35	5·80±1·1 *n* = 10	5·64±0·18 *n* = 53	27·0±0·11 *n* = 58	0·8 *n* = 2
40	—	8·40±1·2 *n* = 22	9·50±0·7 *n* = 46	7·66±0·22 *n* = 30	4·70±0·2 *n* = 52	1·8 *n* = 5
60	—	21·7±3·0 *n* = 13	15·6±0·28 *n* = 35	10·67±0·3 *n* = 30	5·10±0·28 *n* = 37	
70	16 *n* = 2	10·60±1·5 *n* = 18	18·0±0·67 *n* = 24	13·5±3·5 *n* = 21	6·75±0·25 *n* = 20	
80	—	33·7 ±6·0 *n* = 9	29·6 ±1·6 *n* = 15	22·75±1·6 *n* = 8	8·10±0·37 *n* = 32	
90	—	29·5 ±6·0 *n* = 6	21·8 ±1·1 *n* = 12	20·9 ±0·16 *n* = 10	16·7 ±0·47 *n* = 17	
100	—	24·9 ±6·0 *n* = 12	15·37±0·9 *n* = 24	24·0 ±2·1 *n* = 4	14·6 ±0·6 *n* = 20	

— = no larvae were laid.
± = standard error.
n = number of larvae.

TABLE IX.—G. utricularia : *maximum longevity of first instar larvae* (*days*).

Temperature (°C.).	Per cent. relative humidity.								
	0	10	20	40	60	70	80	90	100
16 .	13	17	14	18	33	27	35	32	32
20 .	9	10	10	16	17	23	34	32	24
25 .	6	8	7	10	15	17	29	25	25
30 .	3	5	4	7	7	9	13	18	21

These observations on the winged Fordini confirm those of Broadbent (1949*a*) on *Myzus persicae* and show that the insects are not attracted to their host with the aid of the olfactory sense. Furthermore, the method of transfer can be considered neither a passive migration nor an active one, as described by Kennedy (1950) for *Myzus persicae*. In fact this is not a migration with a definite aim, since the winged forms do not alight on the second host. It is a random distribution of the larvae which find a suitable food plant only if it exists in the neighbourhood by chance.

V. The Winter Generations.

The virgogeniae developed on Gramineae roots differ in their morphology from the fundatrigeniae developing on *Pistacia*. They were in fact described as different genera. Only recently has the identity of these forms been recognised, and it has become clear that the geographical distribution of the winter forms on roots is much wider than the distribution of the genus *Pistacia*. As pointed out by Mordvilko (1928), this distribution indicates that the *Pistacia* was to be found in earlier geological periods wherever the virgogeniae can be found to-day, i.e., as far north as Hamburg and England. With the retreat of the *Pistacia* to the Mediterranean region, the cycle of the aphids was broken and only its Gramineae part persisted as the anholocyclic forms which in the spring spread from plant to plant through winged virgogeniae. Thus, as recognised by Mordvilko (1927, 1928), *Forda formicaria* Heyden represents the anholocyclic form of *F. semilunarius* Pass.; *F. marginata* Koch (see Theobald, 1929 : 186) of *F. follicularia* Pass.; *Paracletus cimiciformis* Heyden of *P. pallidus* Derbès ; *Rhizobius poae* Buckton of *Aploneura lentisci* Pass.

Further studies are certain to establish the specific identity of other forms living on grasses with the winter generations of gall-producing species.

Roberti (1939) reports these winter forms as serious pests to agriculture in Italy. No such cases are known from Israel, where wingless forms on roots are only occasionally found. Rearing experiments in the laboratory were difficult to carry out and only small numbers of aphids attained maturity. Nevertheless from these scant data it was possible to learn the number of generations developing on Gramineae. The generation of virgogeniae obtained from winged forms and reared in February reached maturity under laboratory conditions after 31 to 37 days. Their total longevity was about 70 days. When kept out of doors they reached maturity in 46 to 57 days. Their offspring, either winged or wingless, developed to maturity after 19 to 25 days. It can thus be concluded that only two generations develop in the field in the vicinity of Jerusalem, since in April winged aphids can already be seen returning to the *Pistacia*.

VI. The Winged Sexuparae or Remigrantes.

The flight of these forms generally occurs at the beginning of April but may come much later in years with a late rainy season. They can be observed in large numbers around the *Pistacia* trees for about a fortnight. No experiments could be carried out with these forms, since few aphids could be reared under laboratory conditions, but field observations show that they are in some way attracted to the *Pistacia*, since not one of them was seen to alight on any other tree in the vicinity of *Pistacia* even if they were present in thousands in the surrounding air. The behaviour of these insects is very characteristic. They run over the trunk and the branches and deposit their larvae quickly, while running, one larva at a small distance from the other. Those that have finished laying can easily be recognised by their contracted abdomen. The number of larvae, males and females, varies from 4 to 7. The insects continue to live on the tree for a day or two, but are usually attacked by ants and spiders. Thus the presence of dead aphids in spiders' webs on the tree served to indicate the beginning of the spring remigration.

VII. THE SEXUALES.

These forms are laid on the trunk and the branches at a distance of a few cm. from each other. They are very small, less than 0·5 mm. in length and devoid of mouth-parts. Immediately after being born they moult and enter crevices in the bark in which they settle. This strong thigmotaxis brings together groups of insects scattered by the sexuales on the tree, and permits copulation. The males die after copulation and a single egg develops in each female. The total length of life of males is estimated at 5–6 days, and that of females at approximately two weeks.

The egg.—During the week in which the females attain sexual maturity the egg grows within the female, presumably at the expense of the reserves in the fat body, since the insect does not take any food during this time. The egg continues to grow after copulation till it fills the thorax and the abdomen of the female. About a week after copulation the integument of the female begins to harden and becomes brown or black (this differs in the various species). The process starts in the region of the thorax and spreads towards the abdomen. The female dies during this process and her body assumes the form of a black or brown barrel, while the head and appendages, which remain transparent and unpigmented, dry up. Thus the unlaid egg is protected from desiccation by the darkened and hardened cuticle of the female which is covered by a layer of wax. This is the " cyst " described by Derbès (1869). The egg remains in this form until the following spring, i.e., for about 12 months.

With the coming of the autumnal rains the egg commences to absorb water and to swell, and the protecting integument of the female bursts along the suture between the pro- and mesothorax. In the spring the larva hatches from the egg and leaves the empty shell of the female body behind (figs. 7 and 8).

Groups of these eggs can be found every year under the layer of lichen covering the lower part of the bark of *P. palaestina* and deep in the bark of *P. atlantica*. The empty dried shells of these eggs which consist of the desiccated bodies of the female become imbedded in the bark during its process of growth and can be found with the use of a lens when fragments of bark are broken.

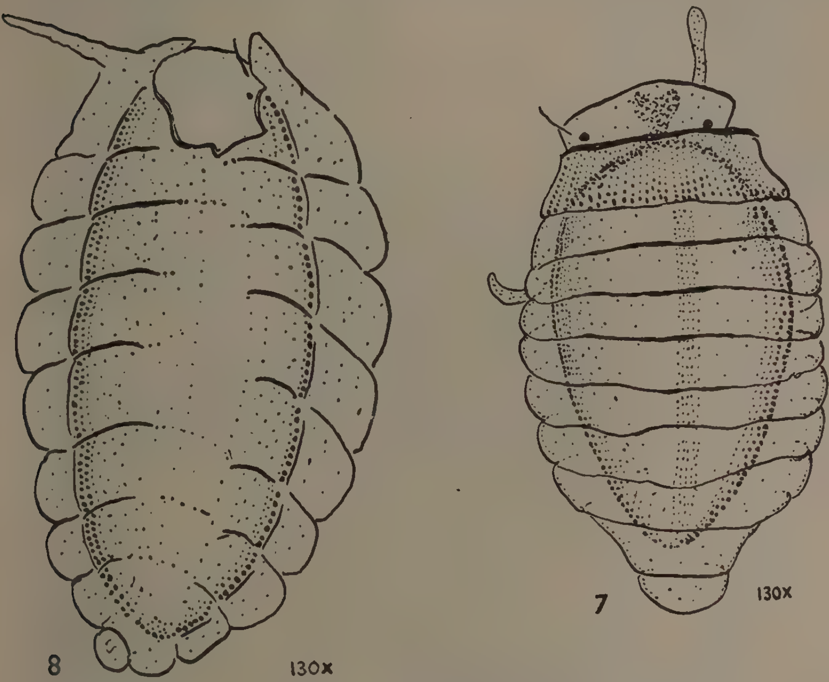
VIII. SUMMARY.

Seven species of aphids belonging to the tribe Fordini produce galls on three species of *Pistacia* in Israel. The life cycle of these insects comprises forms producing galls on *Pistacia* and free living generations developing on Gramineae roots.

The increase in the aphid population within the galls as well as the number of wingless and winged generations was followed by counts carried out in galls picked at random. Reproduction in the galls was found to be viviparous and parthenogenetic. Except for the fundatrix or the first fundatrigeniae there appears to be no mortality in the galls.

The flight of the winged aphids does not occur in the dark under any combinations of temperature and relative humidity. In diffuse light the aphids take to wing at a temperature of 24 to 24·5° C.

As the winged aphids are not attracted by grasses on which their offspring develop during the winter and spring and as their first instar larvae are capable of withstanding long periods of starvation, up to 35 days at a constant tempera-of 16 to 20° C. and a constant relative humidity of 80 per cent., and up to four months in a humid greenhouse with a varying but low temperature, the following picture of the migration from *Pistacia* to grasses appears : the winged aphids disperse in all directions from the tree, but mainly in the direction of air currents. They lay their larvae wherever they find themselves at the termination of the flight. The young larvae stay where they are born in a semidormant state, without movement and without taking any food, until the grass begins to germinate in their vicinity.



Figs. 7–8.—*Forda sp.* (7) Dead, dry body of sexual female containing egg. (8) The egg has absorbed water and the female's skin has burst.

Dedifferentiation of temporary fully grown galls was observed.

Acknowledgment.

The author wishes to express her thanks to Prof. F. S. Bodenheimer for his kind advice and constant interest during the progress of this work.

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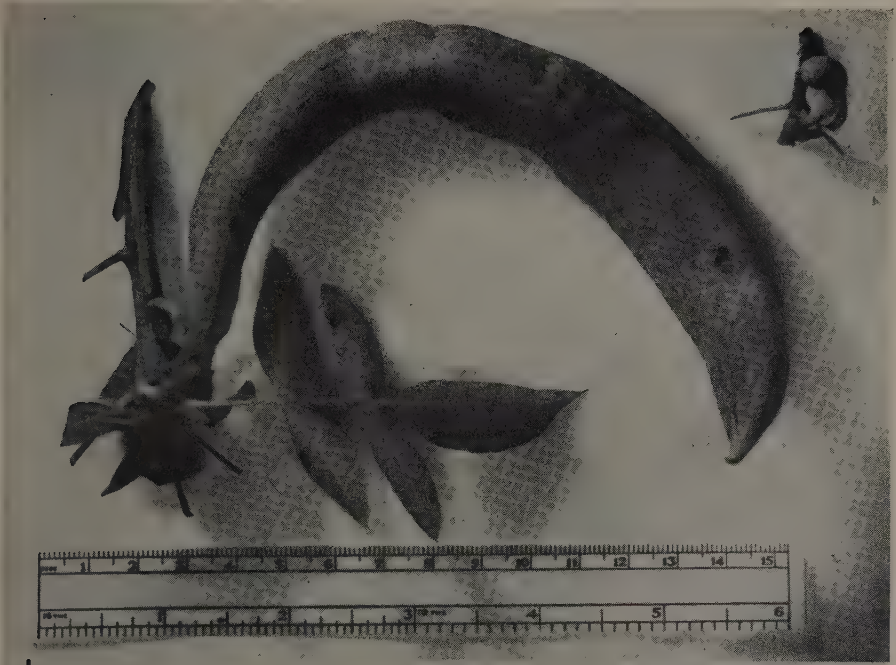
PLATE I.

FIG. 1.—*Baizongia pistaciae* L. Variation in gall size.

FIG. 2.—Gall of *Aploneura* sp. on *P. atlantica* Desf.

PLATE I.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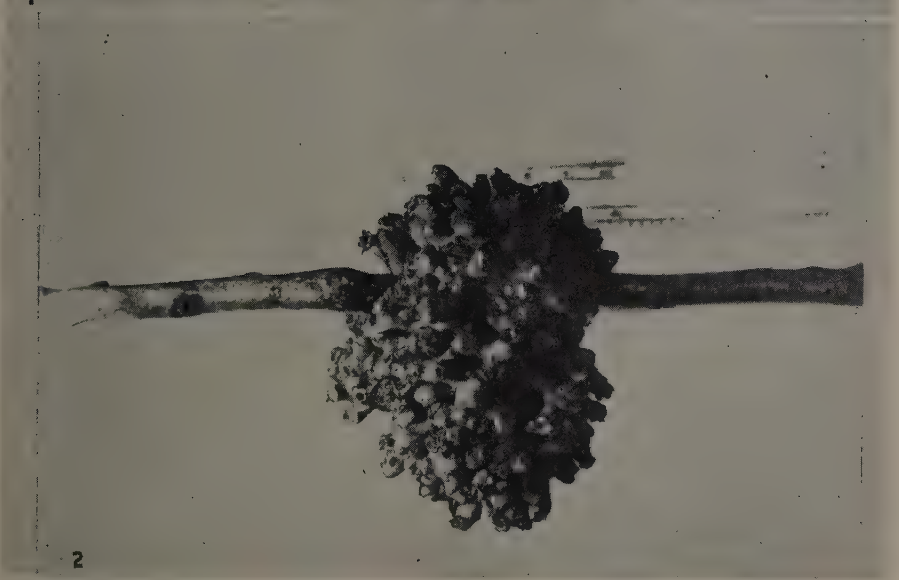

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SOME NOTES ON AND ADDITIONS TO THE DROSOPHILIDAE (DIPTERA) OF SAMOA AND FIJI.

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Manuscript received 13th May, 1953.

(Read 4th November, 1953.)

With 9 Text-figures.

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1. INTRODUCTION.

DURING the period from November 1950 to January 1951, about 1500 flies belonging to the family Drosophilidae were collected in Samoa. From this collection, 764 specimens were mounted for detailed examination. The remainder, which belonged to common species, were examined and preserved unmounted. During this period one specimen was also collected at Suva, Fiji.

An account of the collections is given in this paper.

The sole contribution to our knowledge of the Drosophilidae of Samoa is contained in a paper by Malloch (1934), in which 28 species belonging to ten genera were recorded. Two of these genera, viz. *Hirtodrosophila* Duda and *Spinulophila* Duda, are now included in the genus *Drosophila* Fallén and in this paper a third genus, viz., *Hopkinsomyia* Malloch is reduced to a synonym of *Microdrosophila* Malloch. Two further genera, viz., *Liodrosophila* Duda and *Leucophenga* Mik are recorded here for the first time from Samoa. The total genera of this family known to occur in Samoa therefore remains at ten.

The present collection contained 18 species of the family, ten of which were already known from Samoa. The remaining eight species are new and are described here. With these additions the total number of species of Drosophilidae recorded from Samoa is now thirty-six. One new species was discovered in Fiji and its description is included in this paper because it shows affinities to a Samoan form.

The greater part of the collecting was done on Manono Island. This is a small island within the coral reef and reaches a maximum height of about 200 feet above sea level. Its whole area may be regarded as a typical coastal habitat. Collections were also made at two localities on Upolu, both a few miles from Apia. These were at Vailima (600 ft.) on the lower edge of the rain forest and at Malololelei (2000 ft.). In these two localities collecting was mainly restricted to virgin rain forest well removed from inhabited areas.

As might be expected in a tropical habitat, Drosophilid flies are exceedingly numerous in Samoa. Swarms were always present about fallen fruit and collecting of such flies was easy. Sweeping over foliage and along bush tracks was also productive of many specimens. Traps were seldom used, not because they were inefficient but because it was easier to collect specimens with a net.

An analysis of the mounted collection shows that it is composed of the following:

Drosophila ananassae Doleschall	322	specimens.
D. nasuta Lamb	180	,,
D. bryani Malloch	161	,,
D. hypopygialis Malloch	72	,,
All other species	29	,,

The unmounted portion of the collection consisted entirely of the four named species.

The majority of the specimens were collected by the author. Types of new species are retained in the author's collection.

2. List of Species of Samoan Drosophilidae.

The following is a list of the species of Drosophilidae known to occur in Samoa:

Drosophila seminigra Duda, 1923.
D. unicolor Malloch, 1934.
D. innocua Malloch, 1934.
D. manonoensis sp. n.
D. fuscovittata sp. n.
D. marjoryae sp. n.
D. samoaensis sp. n.
D. excepta Malloch, 1934.
D. bryani Malloch, 1934.
D. melanogaster Meigen, 1830.
D. montium de Meijere, 1916.
D. ananassae Doleschall, 1858.
D. nasuta Lamb, 1914.
D. hypopygialis Malloch, 1934.
D. albifrontata Malloch, 1934.
D. pleurovittata sp. n.
D. convexa Malloch, 1934.
D. nigrifrons Malloch, 1934.
D. upoluae Malloch, 1934.
Leucophenga samoaensis sp. n.
Liodrosophila flavipes sp. n.
Lissocephala versicolor Malloch, 1934.
L. pallidipennis sp. n.
Microdrosophila convergens (Malloch), 1934.
Mycodrosophila nigrithorax Malloch, 1934.
M. buxtoni Malloch, 1934.
M. gratiosa (de Meijere), 1916.
Scaptomyza stamineipes Malloch, 1934.
S. bicolor Malloch, 1934.
Upolumyia pictifrons Malloch, 1934.
U. bimaculata Malloch, 1934.
Samoaia comma Malloch, 1934.
S. hirta Malloch, 1934.
S. nuda Malloch, 1934.
S. ocellaris Malloch, 1934.
Zygothrica samoaensis Malloch, 1934.

The following species is an addition to the Fijian fauna: *Lissocephala fijiensis* sp. n.

3. KEY TO GENERA OF SAMOAN DROSOPHILIDAE

The key given by Malloch (1934) remains satisfactory except for the absence of *Leucophenga*, but a more up to date and comprehensive key has been compiled for the Pacific region, (Wheeler 1952).

The following key is based on Wheeler's key (loc. cit.) but is restricted to Samoan genera.

1. Mesonotum with three pairs of strong dorsocentrals, anterior pair close to suture . . . . **Samoaia** Malloch.
   Mesonotum with one or two pairs of strong dorsocentrals, all post-sutural . . . . 2.
2. Entire front highly polished or with a large glossy central triangle extending to anterior margin and only narrowly separated from the shining orbits; more or less metallic coloured species . . . . 3.
   Not as above, the front usually only slightly shining or dull, the triangle usually small; if metallic coloured in part, then the front is not highly shining . . . . 4.
3. Entire front highly polished; fore femora without a comb of small spines on inner surface . . . . **Lissocephala** Malloch.
   The shining front and orbits separated by a narrow dull line on each side of the triangle; fore femora with a comb on inner apical half or more (?) . . . . **Liodrosophila** Duda.
4. Acrostichal hairs in six or more rows . . . . 5.
   Acrostichal hairs in two or four rows . . . . . . **Scaptomyza** Hardy.
5. Acrostichal hairs in ten or more rows . . . . **Leucophenga** Mik.
   Acrostichal hairs in six or eight rows . . . . 6.
6. Distal costal incision exceptionally deep, the lobe thus formed prominent and black, usually protruding beyond margin . . . . . . 7.
   Costal incision normal, the lobe sometimes dark but not protruding beyond wing margin . . . . 8.
7. All three orbitals large and of about equal size; hind tibia with a distinct bristle about one-third from base on postero-dorsal surface; two pairs of subequal dorsocentrals; mostly pale yellowish species with darker markings . . . . **Upolumyia** Malloch.
   Anterior reclinate orbital usually much smaller than other two; hind tibia without described bristly hair; often with only one pair of dorsocentrals; usually dark species or dark above and contrastingly pale below . . . . **Mycodrosophila** Oldenberg.
8. Proboscis heavily chitinized, stout, straight and downwardly projecting, the apical section often as long as head height; central frontal triangle often distinct, large and subshining; oral margin indented medianly, the cheeks extended forward on either side; orbitals often in nearly straight row and about equally separated at bases . . . . **Zygothrica** Wiedemann.
   Not entirely as above; rarely with any of the above characters . . 9.
9. Anterior dorsocentrals close to suture . . . **Microdrosophila** Malloch.
   Anterior dorsocentrals well separated from suture and close to posterior dorsocentrals . . . . **Drosophila** Fallén.

4. DESCRIPTIONS OF AND NOTES ON THE SPECIES.

Drosophila Fallén, 1823.

The genus *Drosophila* is the largest representative of the family in Samoa. A key to the species of the genus occurring in Samoa is given below. In compiling the key much use has been made of Malloch's (1934) key to species, especially in order to include those species unrepresented in the present collection.

Key to species of the genus *Drosophila* Fallén in Samoa.

1. Third antennal segment large, covered with long hairs . . . . . . 2.
   Third antennal segment normal, covered with short fine pile . . . 5.
2. Costa with a small, distinct, dark mark at apex of first costal section **unicolor** Malloch.
   Costa without small dark mark at apex of first costal section . . . 3.
3. Front, face, upper half of occiput, mesonotum and scutellum black, remainder of insect pale yellow . . . . **seminigra** Duda.
   General colour testaceous to yellow . . . . 4.
4. Basal scutellars equal in length to apical scutellars . **manonoensis** sp. n.
   Basal scutellars just over half length of apical scutellars . **innocua** Malloch.
5. Prescutellar bristles present . . . . 6.
   Prescutellar bristles absent . . . . 10.
6. Scutellar bristles equal or subequal . . . . 7.
   Basal scutellar bristles about half length of apical scutellars **bryani** Malloch.
7. Costal index less than 2·0 . . . . 8.
   Costal index greater than 2·0 . . . . 9.
8. Eyes bare . . . . **samoaensis** sp. n.
   Eyes with dense, short, erect hairs . . . . . . **excepta** Malloch.
9. Eyes bare . . . . **fuscovitatta** sp. n.
   Eyes with dense, short, erect hairs . . . . . . **marjoryae** sp. n.
10. Fore femora with an antero-ventral series of short stout spines **nasuta** Lamb
    Fore femora without such series of short stout spines . . . . . . 11.
11. Arista with 11 or more branches . . . . 12.
    Arista with 10 or less branches . . . . 16.
12. Front densely silvery-white except on orbits and middle line **albifrontata** Malloch.
    Front without dense silvery-white colouration . . . . 13.
13. Vibrissa single . . . . 14.
    Vibrissa duplicated . . . . 15.
14. Light coloured species, black abdomen, bivittate pleura **pleuvovittata** sp. n.
    Entirely dark species, no vittae on pleura . . . . . **nigrifrons** Malloch.
15. Dark brown species; heavy bristles on four fifths of third costal section . . . . **upoluae** Malloch.
    Light coloured species; heavy bristles on half of third costal section **hypopygialis** Malloch.
16. Blackish species . . . . **convexa** Malloch.
    Light coloured species . . . . 17.
17. Acrostichal hairs in six rows . . . . **montium** de Meijere.
    Acrostichal hairs in eight rows . . . . 18.
18. Costal index above 2·0 . . . . **melanogaster** de Meijere.
    Costal index below 2·0 . . . . **ananassae** Doleschall.

Drosophila manonoensis sp. n.

Male.

General : a light yellow species with dark abdomen. Body length about 2·5 mm.; wing length about 2·0 mm.

Head : arista with about six branches, one below in addition to the terminal fork; blackish brown, yellowish-brown basally. Antennae light yellowish-brown; third segment at least twice length of second segment, covered with long, fine, whitish pile and longer hairs on anterior margin; second segment with two bristles. Front yellowish-brown; just less than half width of head at vertex; ocellar triangle between ocelli, brown and distinctly raised. Three strong fronto-orbitals, the ratio of their lengths, anterior to posterior, 3 : 2 : 3, the anterior reclinate closer to proclinate than to posterior reclinate and on the line between these two bristles; row of short hairs on anterior half of frontal orbit extending from anterior reclinate; about four or five small, inwardly directed hairs on either side of anterior median region of front. Face light yellow. Carina narrow and sharply ridged, extending at most two-thirds down face, not sulcate. One strong vibrissa; second oral bristle not differentiated; two bristles at lower angle of cheek. Eyes dark red in pinned specimens; almost bare, with a few, fine, short hairs only. Vertical diameter of eye about eight times width of cheek in same axis. Cheeks yellowish-brown. Proboscis light yellow, brown at lobes; palpi yellowish-brown, one strong apical and one smaller median bristle.

Thorax : yellowish-brown dorsally; yellow laterally. Scutellum yellowish-brown, slightly convex. Acrostichals in about eight irregular rows; no prescutellars; anterior dorsocentral just greater than half length of posterior dorsocentral; basal scutellars divergent and equal in length to apicals; three humerals; two sternopleurals, sterno-index about 0·5.

Legs light yellow. Apical bristles on first and second tibiae, that of second strong; weak preapicals on all three tibiae.

Wings clear; veins light brown; third costal section with heavy bristles on its basal nine-tenths; two bristles at distal costal break, one stronger than the other; costal index about 1·6; fourth vein index about 1·8; 4*c* index about 1·25; 5*x* index about 2·2.

Halteres brown, light yellow basally.

Abdomen : first segment yellowish-brown; remaining segments with yellowish-brown band anteriorly, wide dark brown, uninterrupted band posteriorly. Both bands becoming progressively darker towards posterior segments so that apical segments appear almost completely black.

Type male, SAMOA : Manono Island, 6.xi.1950.

This species is a member of the subgenus *Hirtodrosophila* Duda, but because of the lack of knowledge of some internal characters, and of immature forms, it cannot yet be placed in any species group of the subgenus.

This species brings the number of species of the subgenus known from Samoa to four.

Drosophila bryani Malloch.

D. bryani Malloch, 1934, *Insects of Samoa,* Part VI : 310. (fig. 7; fig. 4.)

The following additional or more precise descriptions of some characters of this species are given below:

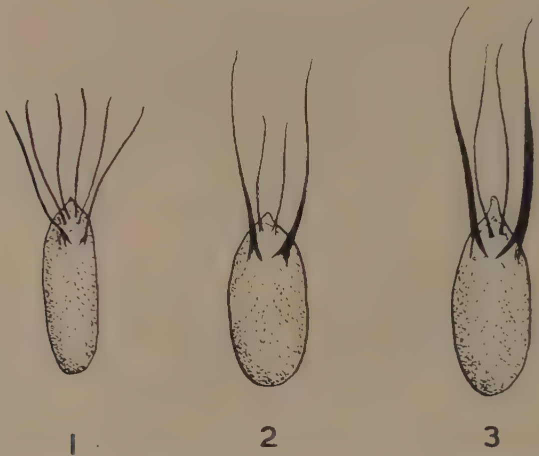
Arista with eight branches, two below in addition to the terminal fork; branches long and slender, bent terminally at tip, those nearest base bent most strongly.

Three prominent sternopleurals, the two dorsal ones equal in length or the anterior of the pair just shorter; ventral bristle below and posterior to the middle one; sterno-index about 0·7–0·75. Basal scutellars convergent. Costal index about 1·65; 4th vein index about 2·3; 4*c* index about 1·4; 5*x* index about 2·5.

External male genitalia have the following characters: Genital arch broad below; densely bristled on lower portion, upper portion with two smaller bristles; ventral margin not concave; heel with horn-like process; toe rounded, broad. Anal plate separated from genital arch; heavily bristled. Clasper without obvious lobe-like process projecting below primary teeth; about 12 primary teeth in a concave row; no secondary teeth.

Eggs with six filaments all approximately equal in length and about three-quarters length of egg.

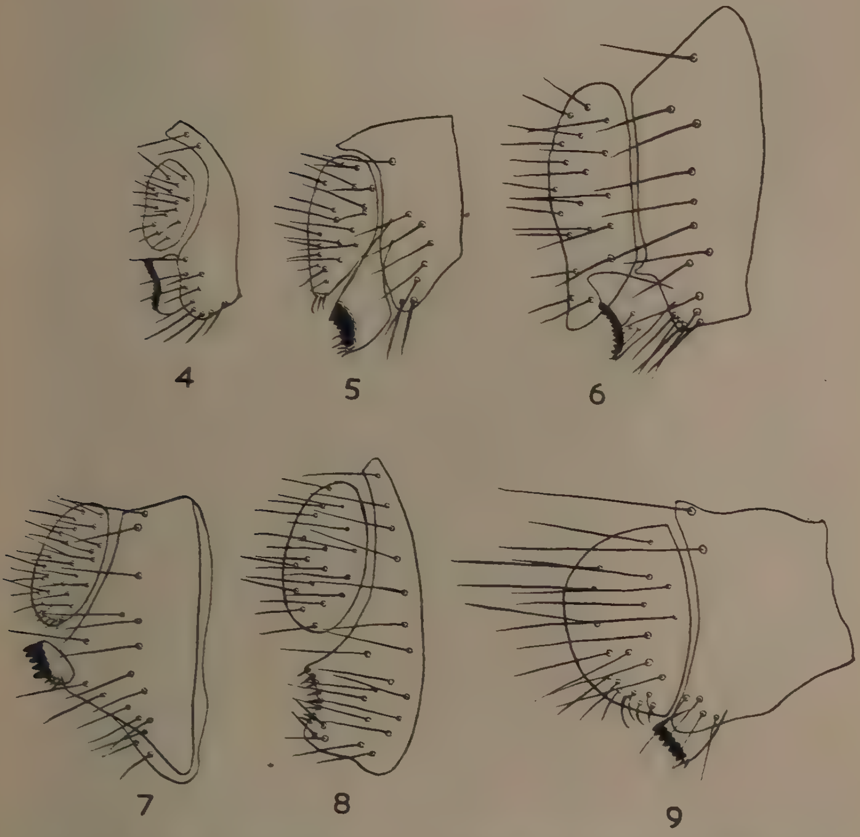
Specimens were collected by sweeping foliage and from rotting fruit at Vailima and Malololelei, Upolu and Manono and Apolima Islands from November, 1950, to January, 1951. 161 specimens were examined but about twice this number were collected.



Figs. 1–3.—Eggs of (1) *Drosophila bryani* Malloch, (2) *D. hypopygialis* Malloch, (3) *D. nasuta* Lamb.

Wheeler (1949) considers that this species possibly belongs to the *victoria* species group of the subgenus *Pholadoris* Sturt. With the knowledge of the above characters its position in this species group is even more certain. The sternopleurals are quite definitely three in number and not two as Malloch (1934) recorded; costal index is below 2·0; 4th vein index is between 2·2 and 2·4; 5*x* index is between 1·4 and 2·4; external male genitalia have a horn-like process on the genital arch, the teeth of the clasper are in a concave row and the arch and anal plate are heavily bristled especially ventrally; egg has six filaments. All these are important subgeneric or species group characters. Two characters, viz., convergent basal scutellars and clasper without obvious lobe-like process projecting below primary teeth, are not in accordance with the present definition of the *victoria* species group. However, in this species the orientation of the basal scutellars is a difficult character to describe and its importance should not be emphasised too much. The clasper character may not prove to be of major importance in separating the species groups.

Because of the lack of knowledge of the internal characters of the adult and of larval and pupal characters, this species cannot yet be placed with certainty in the *victoria* species group.



Figs. 4-9.—Male external genitalia of (4) *Drosophila bryani* Malloch, (5) *D. nasuta* Lamb, (6) *D. hypopygialis* Malloch, (7) *D. samoaensis* sp.n. (8) *D. nigrifrons* Malloch, (9) *D. fuscovittata* sp. n.

Drosophila samoaensis sp. n. (fig. 7).

Male.

General : a small fulvous species. Body length 1·5–2·0 mm. ; wing length 1·25–1·5 mm.

Head : arista with about seven branches, two below in addition to the terminal fork ; blackish-brown, basal segment brown. Antennae yellowish-brown ; third segment covered with fine pile ; second segment with two bristles. Front light golden brown with anterior region and orbits narrowly yellowish-brown; small blackish-brown or reddish-brown spot between or slightly posterior to posterior ocelli; ocellar area between ocelli raised. Three fronto-orbitals, the ratio of their lengths, anterior to posterior, 5 : 2 : 7, the anterior reclinate orbital closer to proclinate than to posterior reclinate; row of small hairs on anterior half of frontal orbit, extending from anterior reclinate; some few, small, inwardly directed hairs in a V-like formation on median front. Face light yellow. Carina distinct, widens slightly ventrally and stops short of epistome, not sulcate. One strong vibrissa; second oral bristle not differentiated, two bristles at lower angle of cheek. Occiput brown. Eyes dark red in pinned specimens; bare. Vertical diameter of eye about 10 times width of cheek in same axis. Cheeks light yellowish-brown. Proboscis yellowish-brown with brown oral lobes; palpi yellowish-brown with about four bristles on anterior margin.

Thorax: yellowish-brown. Scutellum slightly convex. Acrostichal hairs in about six irregular rows; pair of enlarged prescutellars about three quarters length of anterior dorsocentral; anterior dorsocentrals half length of posterior dorsocentrals; basal scutellars parallel or slightly convergent, just larger than apical scutellars and just under half way from base of scutellum to apical scutellars; two humerals; three prominent sternopleurals, the two dorsal ones equal in length, ventral one below and just posterior to middle one; sterno-index about 0·73.

Legs light yellowish-brown, tarsal tips not darkened. Apical bristles on 1st and 2nd tibiae; preapicals on all three.

Wings clear, veins light brown; third costal section with heavy bristles on its basal two-thirds; one differentiated bristle at distal costal break; costal index about 1·75; 4th vein index about 2·35; *4c* index about 1·4; *5x* index about 2·25.

Halteres light yellowish-brown.

Abdomen: yellowish-brown; 4th segment with blackish-brown posterior band narrowed or completely interrupted medianly and widened to almost complete width of tergite laterally; remaining segments completely blackish-brown.

External male genitalia have the following characters: genital arch broad below, not rounded, with a large projecting heel; toe at a higher level than heel; about 14 hairs on lower half, one about one-third way down and two dorsally. Anal plate separated from genital arch; about thirty bristles, shorter and closer together near ventral corner. Clasper small, triangular, a single row of five very stout, strong and prominent teeth arranged in straight or slightly convex row; some strong hairs on lower portion; lower portion does not project beyond lower teeth.

Type male, Samoa: Manono Island, swept off foliage, 6.xii.1950.

Paratypes: three males, same data as type.

This species would appear to be a member of the subgenus *Pholadoris* Sturt. The following characters are in agreement with those of the subgenus; prescutellars present; hairs on front form a V; arista has seven branches, two below; second oral bristle is short; sterno-index is between 0·7 and 0·9; middle sternopleural is well developed; costal index is less than 2·0; 4th vein index is between 2·2 and 2·4; cheek is narrow; middle orbital is short; heavy bristles on basal two thirds of third costal section.

The following characters show that, of the two established species groups, this species is more closely related to the *mirim* group than the *victoria* group. It is a yellowish species with black abdominal markings; anterior scutellars are convergent; cheeks very narrow; bristles on male genitalia not very dense below; clasper small and triangular. One character is not in accord with the definition of the *mirim* species group. There are six and not eight rows of acrostichal hairs. In the series studied the rows are very irregular and the interpretation of this character could be in error.

The important group differentiating characters of the larvae and of the malpighian tubules are not known. This species therefore cannot yet be placed in any species group.

Drosophila marjoryae sp. n.

Female.

General : an entirely yellowish-brown species with brown bristles. Body length about 2·5 mm. ; wing length about 2·25 mm.

Head : arista with about seven branches, two below in addition to the terminal fork ; axis black apically, yellowish-brown basally. Antennae fulvous ; third segment normal ; second segment with two bristles. Front golden yellow, fulvous anteriorly ; about half width of head at vertex ; ocellar triangle between ocelli brown and distinctly raised above level of front. Post-verticals small ; three fronto-orbitals, the ratio of their lengths, anterior to posterior bristle, 10 : 5 : 9, the anterior reclinate just closer to proclinate than to posterior reclinate and just lateral to the line between these two bristles ; row of distinct hairs from anterior reclinate along anterior orbit ; many inwardly directed hairs on most of anterior region of front and on median front almost to ocelli and a pair of almost parallel rows of strong hairs. Face yellowish-grey. Carina narrow dorsally and prominent and nose-like ventrally, not sulcate. Strong vibrissa, no differentiated second oral bristle ; two or three bristles at lower angle of cheek. Eyes dark red in pinned specimens, covered with dense whitish-brown pile. Vertical diameter of eye about ten to twelve times width of cheek in same axis. Cheeks brown. Proboscis predominantly brown ; palpi yellowish brown, with up to four large bristles on anterior margin and many smaller hairs.

Thorax : yellowish-brown except shaded darker region on anterior mesonotum. Scutellum convex. Acrostichals hairs in eight rows ; pair of prescutellars present, about equal in length to anterior dorsocentrals ; anterior dorsocentrals about half length of posterior dorsocentrals ; basal scutellars divergent, just shorter than apical scutellars and placed about half way between latter and base of scutellum ; two humerals ; three prominent sternopleurals of the two dorsal ones the anterior is just larger than the posterior ; ventral one below and slightly posterior to middle one, sterno-index about 0·8.

Legs light yellowish brown, not darkened at tarsal tips. Apical bristles on first and second tibiae ; preapicals on all three ; those of second tibia strong.

Wings clear ; veins yellowish-brown ; third costal section with heavy bristles on its basal two-thirds ; distal costal break without a well-differentiated pair of enlarged bristles ; costal index about 2·3 ; 4th vein index about 1·9 ; 4*c* index about 1·0 ; 5*x* index about 1·1.

Halteres yellowish-brown.

Abdomen : yellowish-brown.

Type female, SAMOA : sealevel, Manono Island, 27.xii.1950

Paratypes : 3 females. Same data as type.

This species is named in honour of my wife who assisted in the tedious task of labelling specimens in this collection.

This species would appear to belong to the subgenus *Pholadoris* Sturt. on the basis of the following characters : Prescutellars are present ; hairs on median front numerous and arranged in a pair of nearly parallel rows ; arista with seven branches, two below ; three strong sternopleurals ; sterno-index between 0·7 and 0·9 ; third costal section with heavy bristles on basal two-thirds ; middle orbital about half other two ; second oral bristle reduced ; cheeks narrow. All these are important subgeneric characters but their combined value is reduced somewhat by the wing indices. In this species the costal index is 2·3 which is higher than any yet recorded for the subgenus. Likewise the 4th vein index of 1·9 is lower than any yet recorded for the subgenus and the $5x$ index of 1·1 is outside the range of those recorded. These differences cannot be regarded as excessive and *D. marjoryae* would appear to be most satisfactorily placed as an unclassified species of the subgenus *Pholadoris*.

Drosophila fuscovittata sp. n. (fig. 9).

Male and Female.

General : a yellowish-brown species. Body length about 2·5 mm.; wing length about 2·0 mm.

Head : arista with about 10 to 12 branches, three or four below in addition to the terminal fork; axis black, yellowish-brown basally. Antennae yellowish-brown; third segment brown on outer and apical margin; second segment with two bristles. Front golden yellow, lighter yellow anteriorly; ocellar triangle not darkened between ocelli, slightly raised above level of front. Three fronto-orbitals the ratio of their lengths, anterior to posterior bristle, 6 : 3 : 8, the anterior reclinate lateral to and level with or slightly anterior to proclinate; some minute hairs on anterior half of orbit anterior to middle orbital; some few inwardly directed strong hairs on anterior median region of front. Face light greyish-yellow. Carina distinctly ridged and extends about two thirds down face, not sulcate. One vibrissa; hairs on cheek strong and second oral bristle slightly longer than remaining hairs; two prominent bristles at lower angle of cheek. Occiput dark brown. Eyes dark red in pinned specimens; bare. Vertical diameter of eye about 10 times width of cheek in same axis. Cheeks light yellow. Proboscis yellowish-brown, rostrum margined with brown anteriorly; palpi yellowish-brown, with about four bristles on anterior margin.

Thorax : yellowish-brown with three longitudinal brown vittae; one vitta extending from dorsal humerus, above notopleural suture, to dorsal of wing base; another broader vitta extending from below humerus, across mesopleura, below wing base to haltere; another vitta extending from behind anterior coxa, through the dorsal half of the sternopleura and across the hypopleura. Scutellum slightly convex. Acrostichal hairs in eight rows; pair of prescutellars present, just longer than anterior dorsocentrals; anterior dorsocentrals under half length of posterior dorsocentrals; basal scutellars divergent, just longer than apical scutellars in length and about one third of distance from base of scutellum to apical bristles; two humerals; three sternopleurals, posterior pair prominent, the posterior bristle of the dorsal pair about twice length of anterior bristle; ventral bristle below and posterior to middle one; sterno-index about 0·4.

Legs light yellowish-brown, tarsal tip not darkened. Apical bristles on first and second tibiae; preapicals on all three tibiae; those of second tibiae strong.

Wings light brown; veins brown, third costal section with heavy bristles on its basal three-quarters; two distinct bristles at distal costal break; costal index about 2·5; 4th vein index about 1·9; $4c$ index about 1·0; $5x$ index about 1·6. Halteres yellowish-brown.

Abdomen : yellowish-brown with tesselated pattern of irregular brown areas on basal three segments and more regular brown areas in the form of posterior bands on tergites of posterior segments. Bristles and hairs on tergites stronger on apical segments. Genital plate of female large, broadly triangular, heavily chitinized dark blackish-brown, with large black teeth, about three on ventral margin and about seven on dorsal edge.

External male genitalia have the following characters: Genital arch not heavily chitinized mostly covered by preceding tergite; heel prominent; toe at higher level than heel; two dorsal bristles and four ventral bristles extending over clasper. Anal plate large; separated from genital arch; many long bristles scattered over its whole surface with slightly bunched shorter hairs at lower corner. Clasper small, triangular; seven or eight distinct black teeth in a straight row; one narrow and one broad short hair at lower corner below teeth.

Type male, SAMOA: Upolu, Vailima, 17.xi.1950.

Paratypes male, same data as type ; female, SAMOA : Manono, 24.xi.1950. This species has several characters which are typical of the subgenus *Pholadoris* Sturt., viz., prescutellars present ; second oral bristle reduced ; three sternopleurals; cheeks narrow; heavy bristles on basal three quarters of third costal section. There are, however, some important characters which are quite distinct from those of the subgenus as understood at the present time. The arista has ten to twelve branches ; sterno-index is 0·4 ; wing indices are different from those defined for the subgenus ; female genital plates are large and distinct. The external male genitalia are not typical of the subgenus ; the clasper agrees well but the anal plate is very much enlarged and densely covered with bristles while the arch is almost bare.

As a result the position of *D. fuscovittata* in the subgenus is very doubtful and it would best be regarded at the present time as unplaced in the genus, but with possible affinities to the subgenus *Pholadoris.*

Drosophila ananassae Doleschall.

D. ananassae Doleschall, 1858, *Nat. Tijd. Ned. Ind.* **17** : 128.
D. errans Malloch, 1934, *Insects of Samoa,* Part VI : 301.

322 specimens were examined and many more were collected. It is of interest to note that no other members of the *melanogaster* species group were obtained. Two other members were recorded by Malloch (1934), viz., *D. melanogaster* Meig. and *D. montium* de Meij. Malloch (loc cit.) gave no indication of the proportions of these three species which he had made available to him but there can be no doubt from the large number of *D. ananassae* in this collection that it is the predominant species of the group in Samoa.

Specimens were obtained at Vailima and Malololelei, Upolu and Manono Island and Apolima Island from November, 1950, to January, 1951.

Drosophila nasuta Lamb (figs. 3 and 5.).

D. nasuta Lamb, 1914, *Trans. Linn. Soc. Lond.* **16** : 346.
Spinulophila nasuta (Lamb) Malloch, 1934, *Insects of Samoa,* Part VI : 311.

The following additional and more precise description of some characters of this species are given :

Male and Female.

Two sternopleurals, often a third small middle bristle dorsal to the posterior bristle and anterior to it ; sterno-index about 0·6. Costal index about 3·4 ; 4th vein index about 1·46 ; 4c index about 0·66 ; 5x index about 1·15.

External male genitalia have the following characters : Genital arch broad at top, narrow and distinctly rounded beneath ; about eight bristles on lower half, two smaller ones near top. Anal plate not attached to genital arch with dense fairly evenly placed bristles, two or three smaller curved bristles at lower corner. Clasper single, with six or seven strong black teeth in a concave row, some fine bristles near lower corner and at the corner a few stout bristles.

Eggs with four filaments ; anterior pair equal to length of egg, posterior longer than egg.

Specimens were collected off foliage and rotting fruit at Vailima and Malololelei, Upolu and at Apolima and Manono Islands, Samoa during November, December, 1950, and January, 1951. About 180 specimens are mounted but many more were captured.

This species is a member of the *immigrans* species group of the subgenus *Drosophila.*

Drosophila hypopygialis Malloch (figs. 2 and 6.).

D. hypopygialis Malloch, 1934, *Insects of Samoa,* Part VI : 307.

The following additional and more precise description of the characters of this species are given.

Male and Female.

Three prominent sternopleurals, rather than two as given in the original description, two dorsal bristles, posterior one about two-thirds length of anterior, ventral bristle below and posterior to middle bristle, sterno-index about 0·7–0·75.

Costa with one strong bristle at distal costal break ; costal index about 3·8 ; 4th vein index about 1·33 ; 4*c* index about 0·60 ; 5*x* index about 1·07.

Acrostichal hairs in eight rows which are usually regular in the female but irregular in the male.

External male genitalia have the following characters : genital arch fairly evenly broad and rectangular below with horn like projection on posterior margin just above clasper ; about 14 bristles with a few of them clustered at posterior lower corner. Anal plate separated from genital arch ; with dense evenly spaced bristles. Clasper single with concave row of about ten black teeth on lower three-fifths of the posterior margin, some stout hairs projecting beyond teeth and bristle-like hairs at lower corner.

Egg with four filaments ; anterior pair about two-thirds length of egg and tapering ; posterior pair about equal to egg length and tapering.

Specimens were collected by sweeping foliage and from rotting fruit at Vailima and Malololelei, Upolu and Manono Islands, Samoa during November, 1950, to January, 1951. Seventy two specimens were collected.

From what is now know of this species it would appear to be a member of the subgenus *Drosophila* Fallén. The following characters are essentially of this subgenus : egg with four filaments, anterior pair tapering ; abdomen with dark posterior bands ; sterno-index greater than 0·5 ; costal index over 3·0. Malloch (1934) suggested an affinity with *Spinulophila nasuta* (Lamb) which we now understand as a member of the *immigrans* species group of this subgenus. *D. hypopygialis* does not have the row of femoral spines which is so characteristic of the species group, but instead has a distinct row of hairs in the normal position of the spines in some specimens. These are slightly stronger than the surrounding hairs. It may be found that the presence of a row of distinct femoral spines need not be a distinguishing characteristic of the group. The external male genetalia show characters of the *immigrans* species group such as the concave row of ten primary teeth on the clasper and the presence of stout bristles on its posterior margin.

D. hypopygialis is best regarded at the present time as a member of the subgenus *Drosophila* without obvious relationship to any species group.

Drosophila pleurovittata sp. n.

Female.

General : a fulvous species with black abdomen and distinct vittae on the pleura. Body length about 2·5 mm. ; wing length about 2·0 mm.

Head: arista with about fourteen branches, three below in addition to the terminal fork which in the type consists of three branches; brownish-black, basal segment yellowish-brown. Antennae yellowish-brown; third segment with relatively long fine, whitish pile giving a matt appearance; second segment with two black bristles and a few short hairs; first segment with small black hairs. Front somewhat shining reddish brown, lighter anteriorly; about half width of head at vertex; ocellar triangle black and raised between ocelli. Three fronto-orbitals, the ratio of their lengths, anterior to posterior bristles, 7 : 3 : 11, the anterior reclinate orbital closer to proclinate than to posterior orbital; some small hairs on anterior half of frontal orbit; no hairs on anterior median region of front. Face yellowish-brown dorsally, grey medianly and whitish-grey ventrally. Carina reduced to a small raised ridge on dorsal third of face, not sulcate. Strong vibrissa; no differentiated second oral bristle; two bristles at lower angle of cheek. Occiput brown, sharply ridged at vertex. Eyes dark red; with minute sparse blackish short hairs. Cheeks linear, yellowish-brown with a black line along lower margin. Proboscis black, yellowish-brown on posterior rostrum; palpi black, stout with black apical bristle and smaller anterior bristles.

Thorax: mesonotum fulvous anteriorly to dark reddish-brown posteriorly; pleura yellowish-brown with one dark reddish-brown vitta from below humerus to wing base and another vitta from behind middle of fore coxa, fringing sternopleura dorsally and extending to near base of the haltere. Scutellum darker than mesonotum, convex. Acrostichal hairs in six rows; no prescutellars; basal scutellars divergent, equal to apical scutellars in length; anterior dorsocentrals two-thirds posterior dorsocentrals; two small humerals; one enlarged hair mediad to presutural; three prominent sternopleurals, the two dorsal ones equal in length; ventral one below and posterior to the middle one, sterno-index 0·7.

Legs yellowish-brown except for fuscous regions on apical third of femora and basal quarter of tibia, of the mid and hind legs; tarsal tip not darkened. Apical bristles on first and second tibiae, that of second particularly strong; preapicals on all three tibiae.

Wings clear but smoky at base; veins light yellowish-brown, darker basally; third costal section with heavy bristles on its basal three-sevenths; two strong bristles at distal costal break; costal index about 3·35; 4th vein index about 1·5; 4c index about 0·66; 5x index about 1·3. Halteres reddish-brown with light yellow pedicel and scabellum.

Abdomen: shining black, some slight grey dusting on tergites of basal three segments.

Type female, SAMOA: Upolu, Malololelei, swept off foliage, 18.xi.1950.

This species is very similar to *D. albifrontata* Malloch especially in shape and general coloration. However, it is regarded as a distinct species on the following morphological grounds: The distinctive white vittae on the front of *D. albifrontata* are lacking; the proboscis is predominantly black; wings are darkened at base, some wing indices show apparent differences; eyes are only sparsely clothed with hairs; legs have dark bands.

Both these species are not yet known well enough to be able to place them in any of the established subgenera. They do show, however, in the possession of relatively long hairs on the third antennal segment, a similiarity to the subgenus *Hirtodrosophila.*

Drosophila nigrifrons Malloch (fig. 8.).

Drosophila nigrifrons Malloch, 1934, *Insects of Samoa,* Part VI: 304.

The following additional characters are given:—

Arista with about thirteen branches, three below in addition to the terminal fork. Three sternopleurals, the anterior dorsal bristle about three-quarters length of posterior dorsal one, ventral bristle below and posterior to middle one; sterno-index about 0·6. Costal index about 3·4; 4th vein index about 1·5; 4*c* index about 0·68; 5*x* index about 1·3.

The male external genitalia have the following characters: genital arch long, narrow dorsally, widens below to quadrangular shape; ventral margin slightly concave; heel lower than toe; about seventeen strong bristles evenly situated over body of arch; about eight smaller stubby light brown hairs on posterior margin; three bristles near lower posterior corner. Anal plate separated from arch; about 17 strong bristles evenly situated on its surface. Clasper absent.

Specimens were collected by sweeping vegetation at Malololelei, Upolu, 18.xi.1950 and at Manono, 5 and 6.xii.1950.

This species is interesting because of the complete absence of a distinctly separated clasper. In this case the clasper may have become indistinguishably fused to the arch. There are no distinct teeth but stout short hairs on the posterior edge of the arch which apparently have taken over the function of clasper teeth.

This species cannot be placed yet with certainty into any subgenus.

Genus *Microdrosophila* Malloch, 1921.

This genus is represented by one species in Samoa.

Microdrosophila convergens (Malloch) (**comb. nov.**).

Hopkinsomyia convergens Malloch, 1934, *Insects of Samoa*, Part VI: 289.

The following additional characters for this species are given:—

Apical scutellars distinctly divergent. Sterno-index about 0·45. Costal index about 1·2; 4th vein index about 4·0; 4*c* index about 2·8; 5*x* index about 4·0.

Specimens were collected at Malololelei, Upolu (2000 ft.) on 18.xi.1950 and Manono Island on 28.xii.1950.

There can be no doubt that *Hopkinsomyia* Mall. is a synonym of *Microdrosophila* Malloch for it agrees with all generic characters as defined for *Microdrosophila* by Malloch (1921) and Sturtevant (1942). Although *M. convergens* is close to the genotype *M. quadrata* (Sturt.) it differs in the number of branches of the arista, the wing indices and possibly the number of acrostichal hairs (eight in *M. quadrata* but six irregular rows in *M. convergens*).

As stated above *M. convergens* has distinctly divergent apical scutellars and this character may become an important generic character when it is known for some other members of the genus.

Leucophenga Mik, 1886.

This genus is well known from many parts of the world. Malloch (1934) suggested the possibility of it occurring in Samoa. It is not common there and only one specimen was obtained.

Leucophenga samoaensis sp. n.

Male.

General: a light brown species with unmarked wings. Body length about 2·5 mm.; wing length about 2·0 mm.

Head : arista with about ten branches, three below in addition to the terminal fork; axis black apically, light brown basally. Antennae light brown; third segment darker brown and covered with thick fine pile; second segment with one median black bristle and some few black hairs; first segment with a few conspicuous hairs on inner margin. Front reddish-gold, lighter anteriorly; under half width of head at vertex; ocellar triangle small, black and raised above level of front between ocelli; orbits brown. Post-verticals small; three fronto-orbital bristles, the ratio of their lengths, anterior to posterior bristle, 11 : 3 : 11, the anterior reclinate closer to proclinate than posterior reclinate and lateral to it, proclinate and posterior reclinate relatively close; some small hairs in a line from anterior reclinate anteriorly along orbit; inwardly directed small hairs on a narrow area from ocelli, to middle of anterior margin of front. Face light brown. Carina almost entirely absent and discernible only dorsally. Strong vibrissae present; second oral bristle not differentiated. Eyes dark red in pinned specimen; bare. Cheeks light yellowish-brown; linear. Proboscis yellowish-brown; palpi brownish-black, curved, with one apical bristle and several smaller and finer hairs anteriorly.

Thorax : mesonotum light reddish-brown, somewhat shining, pleura lighter. Scutellum coloured as for mesonotum, convex. Acrostichals hairs in about ten irregular rows; prescutellar acrostichals all enlarged, middle pair very strong about one and one-third times length of anterior dorsocentral; basal scutellars divergent, 1·5 times as long as apical scutellars; anterior dorsocentrals two-fifths posterior dorsocentrals; one humeral; two sternopleurals, sterno-index about 0·8.

Legs light yellow, not darkened at apical tarsal segments. Apical bristles on first and second tibiae, that of first short; preapicals on all three tibiae; mid tarsi with row of closely adherent short stout spinules along entire length of each segment on posterior ventral and anterior ventral surfaces.

Wings slightly pointed; clear but marginal cell somewhat darkened; veins all light yellowish-brown; costa ending at apex of third vein; third castal section with heavy bristles on its basal two thirds and small black wart-like protuberences on the underside; pair of slightly enlarged bristles at distal costal break; costal index about 2·5; 4th vein index about 2·0; 4*c* index about 1·2; 5*x* index about 1·5.

Halteres light brown.

Abdomen : basal segment light brown; second segment light reddish-brown interrupted by black area about the incurving edge of the tergite; third segment same, but the black areas are shifted to the lateral margin of the tergite and a small black spot at the middle of the posterior margin; fourth segment black with a small indefinite yellowish-brown area on anterior median region of tergite; remaining segments black.

Type male SAMOA : Manono Island, swept off foliage, 6.xii.1950.

The above species constitutes the first record of the occurrence of the genus *Leucophenga* in Samoa. The species is quite distinctive with its blackish palpi, almost clear wings which are somewhat pointed, and the abdominal colour pattern. It would appear to be closely related to *L. guttiventris* de Meijere, a species which has been found in Fiji as well as elsewhere in Australian region.

Lissocephala Malloch, 1929

Key to the species of the genus *Lissocephala* Malloch occurring in Samoa and Fiji.

1. Wings with dark basal transverse streak . . . . 2.
–. Wings without black basal streak . . . . **pallidipennis** sp. n.
2. Knob of halteres black . . . . **versicolor** Malloch.
–. Knob of halteres light reddish-brown . . . . . . **fijiensis** sp. n.

Lissocephala versicolor Malloch.

L. versicolor Malloch, 1934, *Insects of Samoa*, Part VI : 287.

The following additional characters are given :—

Pair of slightly enlarged prescutellar hairs. Sterno-index about 0·9. Costal index about 0·8 ; 4th vein index about 2·0 ; 4*c* index about 1·7 ; 5*x* index about 2·25. Dark streak at base of wing commences on the costa at either side of the distal costal break.

Specimens were collected by sweeping foliage at Samoa : Upolu, Vailima, 17.xi.1950 and at Manono Island, 28.xi.1950, and taken on rotting fruit Samoa : Manono Island, 26.xii.1950.

Drosophila metallescens de Meij., as Malloch (1934) suggested, would appear to be a *Lissocephala*. From its description, it is related to *L. versicolor* but is probably closer to *L. fijiensis*.

Lissocephala fijiensis sp. n.

Female.

General : a glossy light reddish-brown species. Length of body about 2·25 mm. ; length of wing about 1·75 mm.

Head : arista with about seven branches ; three below in addition to the terminal fork ; dark brown, light brown basally. Antennae light reddish-brown ; third segment a shade darker apically and covered with distinct fine pile ; second segment with two strong bristles and strong hairs. Front glossy, dark reddish-brown posteriorly, brown anteriorly and medianly ; about half head width at vertex. Post-verticals short ; three fronto-orbitals, the ratio of their lengths, anterior to posterior, 5 : 3 : 8, the anterior reclinate lateral to and level with or just anterior to proclinate ; few hairs on anterior half of frontal orbit ; some inwardly directed hairs on anterior region of front. Face brown. Carina narrow but prominent, ending abruptly before epistome ; not sulcate. One strong vibrissa ; second oral not differentiated ; two fine bristles at lower angle of cheek. Eyes brownish-red in pinned specimens, with thin short brown pile. Cheeks linear, brown. Proboscis light reddish-brown ; palpi light brown with one strong and two weaker bristles in a cluster near apex.

Thorax : entirely glossy, light reddish-brown with slight metallic violet hue. Scutellum dull brown, not markedly dusted at apex, almost flat. Acrostichal hairs in about six rows ; pair of slightly enlarged hairs in prescutellar region ; basal scutellars parallel or slightly convergent, about half length of apicals ; one humeral ; two sternopleurals, sterno-index about 1·0.

Legs light yellowish-brown, tarsal tip not darkened. Fore tibiae with weak apical and preapicals ; mid tibiae with strong apical and preapicals ; hind tibiae with strong preapicals only.

Wings clear with narrow blackish band extending from distal portion of first costal section diagonally across first vein and back through posterior cells to alular region ; veins light brown ; costa strong to a point just beyond apex of third vein, hence very weak to apex of fourth vein ; third costal section with heavy bristles on its basal five-sixths ; pair of bristles at distal costal break, one stronger than the other ; costal index about 0·7 ; 4th vein index about 1·7 ; 4*c* index about 1·7 ; 5*x* index about 1·75.

Halteres light reddish-brown,

Abdomen : glossy light reddish-brown to dark brown with faint metallic hues in some lights.

Type female, Fiji : Suva, Botanical Gardens, swept off grass, 14.xi.1950.

This species is close to *L. versicolor* Mall. The two species are readily distinguished by means of the key but they also differ in general coloration, particularly on the thoracic pleura, and in the wing vein indices such as the fourth vein and 5*x* indices.

Lissocephala pallidipennis sp. n.

Female.

General: a small shining brown species with clear unmarked wings. Body length about 1·5 mm.; wing length about 1·75 mm.

Head: arista with about nine branches, three below in addition to the terminal fork; brownish-black. Antennae brown; third segment blackish-brown apically and dorsally, covered with distinct fine pile; second segment with two bristles and distinct hairs. Front glossy shining brown with large ocellar triangle extending to anterior margin of front. Ocellars and verticals long; post-verticals short; three fronto-orbitals, the ratio of their lengths, anterior to posterior, 13 : 2 : 12, the anterior reclinate much closer to proclinate than to posterior reclinate. Face brown and somewhat shining. Carina slightly developed dorsally and only differentiated about one third distance down face, not sulcate. One strong vibrissa present; no differentiated second oral bristle. Eyes dark red in pinned specimen; covered with distinct dark pile. Vertical diameter of eye at least 10 times width of cheek in same axis. Cheeks light brown. Proboscis yellowish-brown; palpi dark brown and with one strong bristle near apex and other weaker bristles on anterior margin.

Thorax: glossy light brown dorsally and laterally as far as the dorsal margin of sternopleura, hence light yellowish-brown. Scutellum also glossy light brown with, however, some light dusting; markedly convex especially at margin. Acrostichal hairs in about eight irregular rows; no prescutellars; anterior dorsocentral just over half length of posterior dorsocentral; basal scutellars divergent and equal in length to apical scutellars; two humerals; two sternopleurals, sterno-index about 0·5.

Legs light yellowish-brown; tarsal tip not darkened. Apical bristles on first and second tibiae, that of first minute, that of second very strong; preapicals on all three tibiae, that of first minute, that of second strong.

Wings clear, without darkened veins or dark stripes; veins light yellowish-brown, third costal section with heavy bristles on its basal two-thirds; one strong bristle at distal costal break; costal index about 0·85; 4th vein index about 2·5; 4*c* index about 2·2; 5*x* index about 2·75.

Halteres brown.

Abdomen: shining light brown with some slight greyish dusting.

Type female, SAMOA: Upolu, Vailima, 17.xi.1950.

This species is similar and apparently related to *L. versicolor* Mall., but it is readily distinguished by the lack of the black stripe at the base of the wing.

Liodrosophila Duda, 1922.

This genus is close to *Lissocephala* Malloch but is readily separated from it by having the front not entirely glossy.

Liodrosophila flavipes sp. n.

Male.

General: a shining black fly with light yellowish legs. Body length about 2·25 mm.; wing length about 2·25 mm.

Head : arista with about fifteen branches, four below in addition to the terminal fork; black. Antennae blackish-brown; third segment with fine short pile which is larger and tuft-like apically; second segment with brown area on apical dorsal region, two black bristles and some long hairs on inner apical margin. Front with large ocellar triangle reaching anterior margin, shining black; orbits shining black; dull stripe between triangle and orbits narrowed to vertex; over half width of head at vertex. Three fronto-orbitals, the ratio of their lengths, anterior to posterior, 7 : 2 : 12, the anterior reclinate orbital closer to proclinate than posterior reclinate; few small hairs on anterior half of frontal orbit; no hairs on anterior median region of front. Face shining blackish-brown. Carina reduced and only present on dorsal half of face, not sulcate. One strong vibrissa; second oral bristle not differentiated; two bristles at lower angle of cheek. Eyes reddish-brown in pinned specimens; with fine short and sparsely situated hairs. Cheeks dark brown and linear. Proboscis brown to dark-brown with blackish-brown lobes; palpi dark brown with one strong apical and two smaller bristles on anterior margin.

Thorax : entirely shining blackish-brown with some dusting but yellowish ventrally. Scutellum slightly convex. Acrostichals in four rows; no prescutellars; anterior dorsocentrals about two-thirds posterior dorsocentrals; basal scutellars divergent close to base of scutellum and equal in length to the apicals; two humerals; three prominent sternopleurals, the posterior dorsal one larger than anterior dorsal, ventral one below and posterior to middle one, sterno-index about 0·5.

Legs light yellow, tarsal tip not darkened. Apical bristles on first and second tibiae, that of second very strong; preapicals on all three tibiae, that of second also very strong.

Wings clear; veins light brown; third costal section with heavy bristles on its basal two-fifths; pair of strong bristles at distal costal break, costa extends to fourth vein; costal index about 3·8; 4th vein index about 1·65; 4*c* index about 0·65; 5*x* index about 1·5.

Halteres yellowish-brown basally, more fulvous apically.

Abdomen : shining dark brown dorsally; bristly.

Type male, SAMOA : Upolu, Malololelei, swept off foliage, 18.xi.1950.

This species is placed in the genus *Liodrosophila* Duda because of the distinctive characters of the front. In this species, however, the row of stout spines on the antero-ventral surface of the fore femora is absent. This character has heretofore been regarded as an important character of the genus, especially as a means of distinguishing between it and *Lissocephala* Mall., but when further information about the genus is obtained this character may be relegated to one of subgeneric value.

It can be noted here that *Liodrosophila australis* Mall. is almost certainly a *Lissocephala* and is very similiar to *Lissocephala versicolor* Mall. and *L. fijiensis* and *Drosophila mettalescens* de Meij.

Zygothrica Wiedemann, 1830.

Zygothrica samoaensis Malloch.

Z. samoaensis Malloch, 1934, *Insects of Samoa*, Part VI : 278.

The following additional and more precise description of some characters of this species are given :—

Eyes with a covering of fine very short and sparsely situated hairs. Sterno-index about 0·55. Costal index about 2·0; 4th vein index about 1·9; 4*c* index about 1·1; 5*x* index about 1·6. Third costal section with heavy bristles on its basal half.

One specimen was collected by sweeping foliage at SAMOA : Upolu, Vailima, 17.xi.1950.

Samoaia Malloch, 1934.

Samoaia ocellaris Malloch.

S. ocellaris Malloch, 1934, *Insects of Samoa*, Part VI : 271.

Additional characters for this species are :—

Sterno-index about 0·6. Costal index about 2·2 ; 4th vein index about 0·5 ; 4*c* index about 1·0 ; 5*x* index about 0·5. Third costal section with heavy bristles on its basal half.

Specimens were collected by sweeping along bush track, SAMOA : Malololelei, 2000 ft., and at Vailima, Upolu, 17 and 18.xi.1950.

Samoaia hirta Malloch.

S. hirta Malloch, 1934, *Insects of Samoa*, Part VI : 275.

Additional characters for this species are :

Sterno-index about 0·6. Costal index about 1·8 ; 4th vein index about 1·4 ; 4*c* index about 1·1 ; 5*x* index about 1·3. Third costal section with heavy bristles on its basal two-thirds.

One specimen was collected by sweeping vegetation at SAMOA : Malololelei, 2000 ft., Upolu, 18.xi.1950.

5. DISCUSSION.

As no attempt was made to culture the species, this study of the Drosophilid fauna of Samoa has been a morphological one. Thus some important characters are lacking for all species and as a result it has been impossible to place the majority of species into their species group or subgenera with certainty. Where specimens were collected in sufficient numbers, however, to allow dissections of male external genitalia and the recovery of eggs from ovipositors and ovaries, it has been possible to assign such species with more accuracy to their proper positions in their genera.

Thus in the Samoan members of the genus *Drosophila* there are four members of the subgenus *Hirtodrosophila*, five possible members of the subgenus *Pholadoris*, three of the *melanogaster* species group of the subgenus *Sophophora*, one of the *immigrans* species group of the subgenus *Drosophila* and some unclassified species.

Morphological characters satisfactorily distinguish the subgenus *Hirtodrosophila* and it is of great interest that Samoa has four members of a total of 27 known for the world. One of the most interesting facts is the presence of so many species which appear to belong to the subgenus *Pholadoris*. This subgenus has recently been surveyed by Wheeler (1949) and he recorded a total of nine described species as well as some as yet undescribed. There are indications that this subgenus is also well represented inNew Zealand (unpublished data). These facts may indicate that in the South Pacific a sizeable proportion of the Drosophilid fauna has developed from the *Pholadoris* division of the genus.

The analysis of the collection shows that the predominant Drosophilids in Samoa during November to January are *D. ananassae*, *D. nasuta*, *D. bryani* and *D. hypopygialis*. Collection records show that all are common in the coastal region about domestic habitats. Other species are less common. The figures may have been influenced by the great ease in collecting the four common species as they are all feeders on rotting fruit and thus plentiful in the coastal plantations.

Our knowledge of the Samoan Drosophilidae is far from complete. There are undoubtedly more species awaiting discovery, more particularly, perhaps, in the inland rain forest areas. In addition most species need to have many more of their characters described before their taxonomy is fully understood.

6. ACKNOWLEDGMENTS.

The collections were made while the author was a member of a medical research expedition to Samoa. This expedition was organised and financed by the Medical Research Council of New Zealand. Grateful acknowledgments and thanks are extended to the Council for the privilege and opportunity of visiting Samoa.

Thanks are extended to Dr. J. Armstrong, Apia Hospital, Samoa, for organising and facilitating collecting trips to various localities.

Acknowledgment is also made of the assistance of the British Museum (Natural History) in lending specimens for purposes of comparison.

7. SUMMARY.

Notes on a collection of Drosophilidae made in Samoa from November 1950, to January 1951, are given.

Additional or corrected taxonomic characters are given for the following species: *Drosophila bryani* Mall., *D. nigrifrons* Mall., *D. nasuta* Lamb, *D. hypopygialis* Mall., *Microdrosophila convergens* Mall., *Lissocephala versicolor* Mall., *Zygothrica samoaensis* Mall., *Samoaia ocellaris* Mall. *S. hirta* Mall.

The following new species are described: *Drosophila manonoensis*, *D. fuscovittata*, *D. marjoryae*, *D. samoaensis*, *D. pleurovitatta*, *Leucophenga samoaensis*, *Lissocephala pallidipennis*, *Liodrosophila flavipes*.

The following new species from Fiji is also described: *Lissocephala fijiensis*.

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Vol. 105. Part 7. Pp. 117–130. 7 figs. 25th June, 1954

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OSMOTIC REGULATION IN THE LARVAE OF *HELODES* (COLEOPTERA : HELODIDAE).

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Manuscript received 26th September, 1953.
(Read 4th November, 1953.)

With 7 Text-figures.

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Introduction.

It is known that different groups of insects have independently invaded aquatic environments. These have overcome the physiological difficulties presented to them by the new environment in a variety of ways, and it therefore seems possible that the problem of osmotic regulation will not have been solved in precisely the same way by all aquatic insects. Most of our knowledge about osmoregulation in aquatic insects is based on studies of various Diptera (e.g., *Aedes*, *Culex*, *Chironomus* and *Corethra*). Apart from this one Order of insects, there is only the work of Backmann (1911, 1913) on Libellulids and Dytiscids, Claus (1937) on *Sigara*, Beadle and Shaw (1950) on *Sialis*, and Schoffeniels (1950) on *Aeshna* and *Libellula*, and it is clearly desirable to know more about osmoregulation in groups other than the Diptera. In this paper an account is given of experiments on the osmotic regulation of the larvae of two species of *Helodes* (Coleoptera : Helodidae). The larvae of this family have anal papillae. Similar structures in the Diptera appear to function chiefly as salt absorbing organs (Koch, 1938; Ramsay, 1953).

II. Material.

The larvae of two species of Helodidae, *Helodes minuta* L. and *H. marginata* F., were used in this investigation. Both species were taken from a fast-flowing stream at Failand in Somerset, where they were found in the less turbulent parts and beneath stones. Fresh material was used in all experiments.

III. Methods.

To collect samples of the haemolymph for analysis, the larvae were first partially anaesthetised by bubbling CO_2 through the water and then dried on filter paper. A hydrofuge surface was made on the dorsal part of the abdomen by painting it with acetone, followed by a layer of bees' wax dissolved in ether (Beadle and Shaw, 1950). When the abdomen was pricked with a fine needle, the haemolymph could be forced out in the form of a discrete drop. The haemolymph was then collected under a binocular microscope in fine capillary pipettes.

The haemolymph chloride was analysed according to the method of Wigglesworth (1947). By lining the capillary pipettes with a silicone fluid (D.C. 1107) the haemolymph could be handled with ease, and for the same reason the micropipettes and burettes used for all other liquids were also lined with silicone.

The osmotic pressure was determined to ± 0·01 per cent. NaCl by the method of Ramsay (1949). It was found that short exposures of the haemolymph to the air caused a marked rise in osmotic pressure, and the blood was therefore collected as rapidly as possible. Total osmotic pressures and chloride concentrations of the haemolymph are expressed as mM equivalent NaCl.

In view of the objections raised by Heilbrunn and Hamilton (1942) to methods of tissue chloride analysis involving wet ashing with nitric acid, the micro-diffusion method of Conway (1950) was used. The tissues were deproteinised using the method of Folin and Wu (1919). For this method, two larvae were thoroughly dried on filter paper and weighed, they were then homogenised with 1 ml. of water in a tissue homogeniser; 0·2 ml. of 1·0 per cent. tungstate and 0·2 ml. of 0·0667 $(NH_2)_2SO_4$ were then added, and the mixture was again homogenised. The fluid was centrifuged until a perfectly clear supernatant was obtained. One ml. of this was placed in the outer chamber of a Conway micro-diffusion unit (size No. 2A), and the procedure used was that given by Conway for micro-determination of chloride below 35 μg. Cl. The amount of chloride was finally determined colorimetrically using a Hilger's Spekker absorptiometer.

The effect of deproteinising by the method of Folin and Wu was investigated in order to determine the correct concentrations of sodium tungstate and sulphuric acid to be used to obtain the maximum recovery of chloride. To do this 21 larvae of *H. marginata* were homogenised in 7 ml. of glass distilled water. One ml. samples were then taken, and varying total concentrations of sodium tungstate and sulphuric acid were added to each. Equal proportions were used in each sample. The chloride recovery in each is given in fig. 1. It will be seen that the addition of the deproteinising reagents greatly increased the amount of chloride recovered. From these results it would seem that an excess of the deproteinising reagents causes a slight fall in the recoverable chloride, and that it is essential to have the reagents at the correct concentration.

The above method gave a 99 per cent. recovery of added chloride. The total body chloride is expressed as mg. Cl./gram of tissue (wet weight).

For some experiments it was essential to find a way of blocking the anal papillae and mouth. It was not possible to use ligatures with these insects, but a small drop of Whitehead's Varnish applied to the mouth or the papillae acted as a satisfactory block. To do this the insect was held gently in a short length of glass tubing by a piece of plasticine so that the tip of the abdomen was held steady. A drop of the varnish was then applied with a loop of very fine wire to the papillae or mouth. This operation was carried out under the high power of a binocular microscope. The varnish seemed to have no serious toxic effects on the larvae. Larvae with the varnish applied to various parts of the body were still alive after fourteen days.

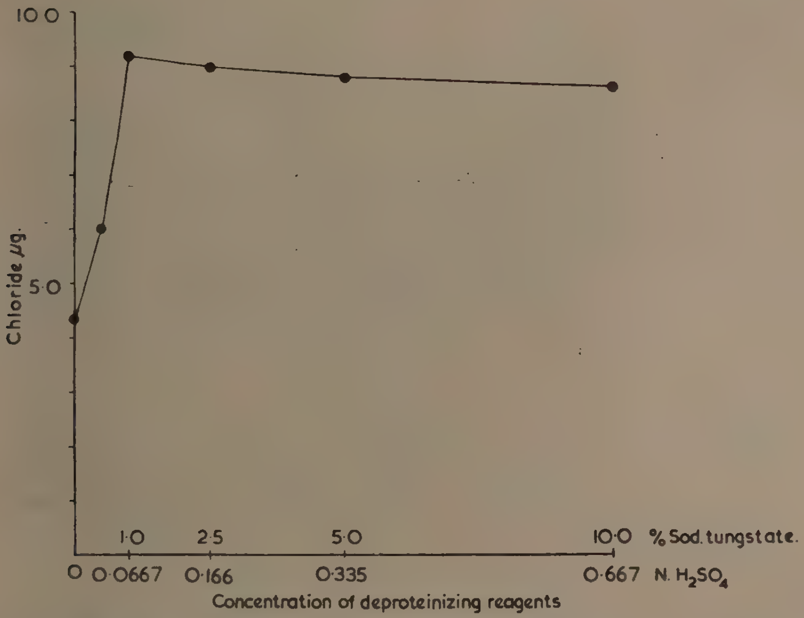

FIG. 1.—The effect of concentration of the deproteinising reagents on the recovery of chloride.

IV. RESULTS.

a. *Regulation of the Osmotic Pressure and Chloride of the Haemolymph.*

The normal osmotic pressure of the haemolymph of *H. marginata* varied between 154 and 167 mM NaCl with a mean of 161 mM (0·94 per cent. NaCl),

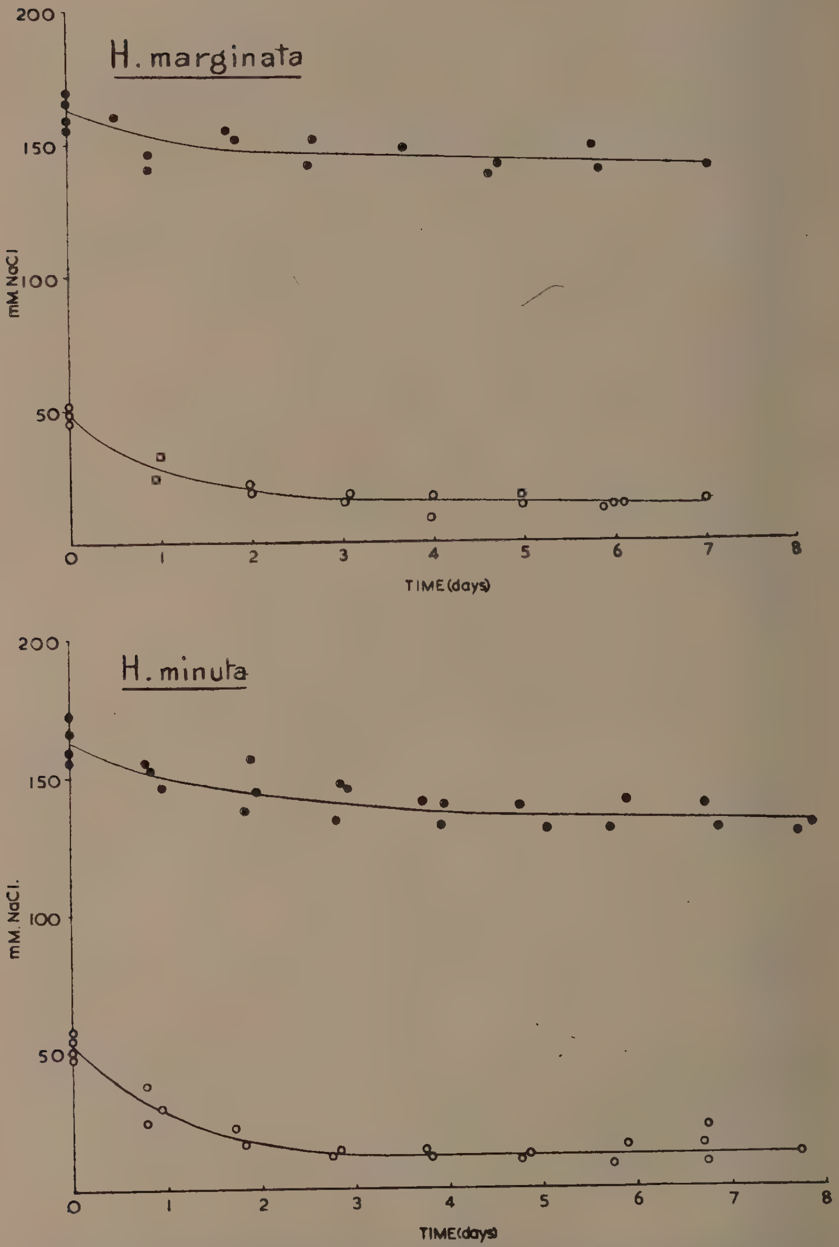

Fig. 2.—The effect of starvation in glass distilled water on the osmotic pressure (closed circles) and chloride concentration (open circles) of the haemolymph of *H. minuta* and *H. marginata*.

while that of *H. minuta* varied between 155 and 171 mM NaCl with a mean of 162 mM (0·95 per cent.).

The chloride concentration of the haemolymph of *H. marginata* ranged from 46 to 49 mM (mean of 48 mM). That of *H. minuta* ranged from 48 to 56 mM NaCl, with a mean of 52 mM NaCl. The chloride concentration of the haemolymph, therefore, accounts for approximately 30 per cent. of the total osmotic pressure.

The larvae of both species when starved in glass distilled water at 15·0 (± 0·5)° C. showed a fall in osmotic pressure and in the concentration of chloride in the haemolymph. In both species the haemolymph chloride fell rapidly within three days to a basal level of approximately 14 mM (fig. 2). The osmotic pressure fell more gradually than the chloride, reaching a value of approximately 144 mM NaCl after seven days. It is therefore clear that the curve for the chloride concentration falls more rapidly than the one for osmotic pressure, which indicates that in both species the non-chloride fraction of the blood is capable of some regulation of the total osmotic pressure.

When larvae of *H. minuta* were starved in well aerated Failand stream water (0·35 mM NaCl) at 15·0° C., there was a mean fall in osmotic pressure of 8 mM NaCl after three days and 9 mM NaCl after seven days. The chloride concentration of the haemolymph, however, fell by 17 mM NaCl after three days and 25 mM NaCl after seven days. The larvae cannot, therefore, maintain the normal chloride concentration of the haemolymph when starved in stream water, although there appears to be some regulation of the osmotic pressure, which does not fall to the same extent as the chloride concentration. These results are shown in Table I.

Table I.

Time.	Cl (mM NaCl).	Mean.	Mean fall in Cl.	O.P. (mM NaCl).	Mean.	Mean fall in O.P.
—	55 56 48 48	52		164 155 171 157	162	
3 days	34 44 34 29	35	17	— 154 156 151	154	8
7 days	24 23 34 27 29	27	25	157 147 152 152 156	153	9

Fig. 3 shows the effect of starvation in glass distilled water on larvae of *H. minuta* which had their mouths blocked with varnish. It will be seen that there was no detectable fall in osmotic pressure during the period of the experiment, and that there was only a slight fall in the chloride concentration of the haemolymph. The broken lines indicate the fall obtained with normal larvae kept under the same conditions (data from fig. 2).

b. *Permeability to Chloride.*

Larvae of *H. minuta* kept in a balanced salt solution (Wigglesworth, 1938) equivalent to 137 mM NaCl survived for about four or five days. From fig. 4 it will be seen that larvae starved in this solution showed a rise in osmotic pressure and a greater rise in haemolymph chloride. The larva is, therefore, permeable to chloride ions. The non-chloride fraction of the haemolymph is able to compensate to some extent for an increase in the chloride concentration, for although the chloride showed an increase of about 60 mM NaCl, the total osmotic pressure only rose by approximately 26 mM NaCl.

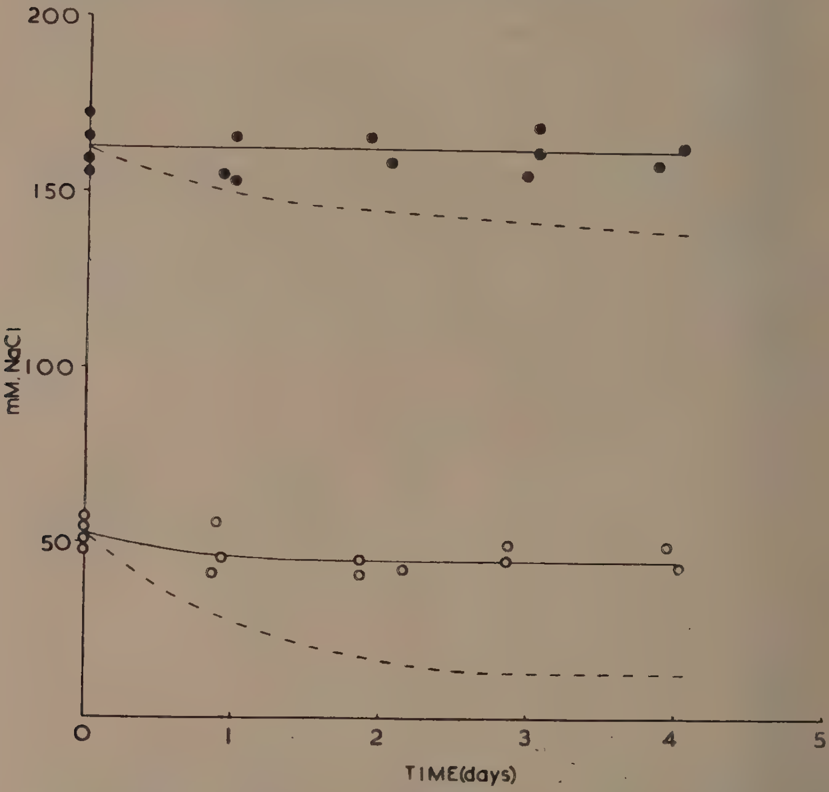

Fig. 3.—The effect of starvation in glass distilled water on the osmotic pressure (closed circles) and the chloride concentration (open circles) of the haemolymph of larvae of *H. minuta* with their mouths blocked. The broken lines indicate the fall obtained with normal larvae (fig. 2).

In larvae in which the mouths were blocked there was a less rapid increase in chloride concentration, while larvae with the mouth and anal papillae blocked showed no appreciable increase in concentration. The general body surface is therefore relatively impermeable to any inward diffusion of chloride, the gut and the anal papillae forming the most important chloride permeable surfaces.

c. *Loss and Uptake of Chloride Ions.*

In these experiments all the analyses were made for total body chloride, the changes in concentration of haemolymph chloride being too small for a satisfactory investigation of the exchange of Cl ions. Larvae of *H. marginata* were used in these experiments.

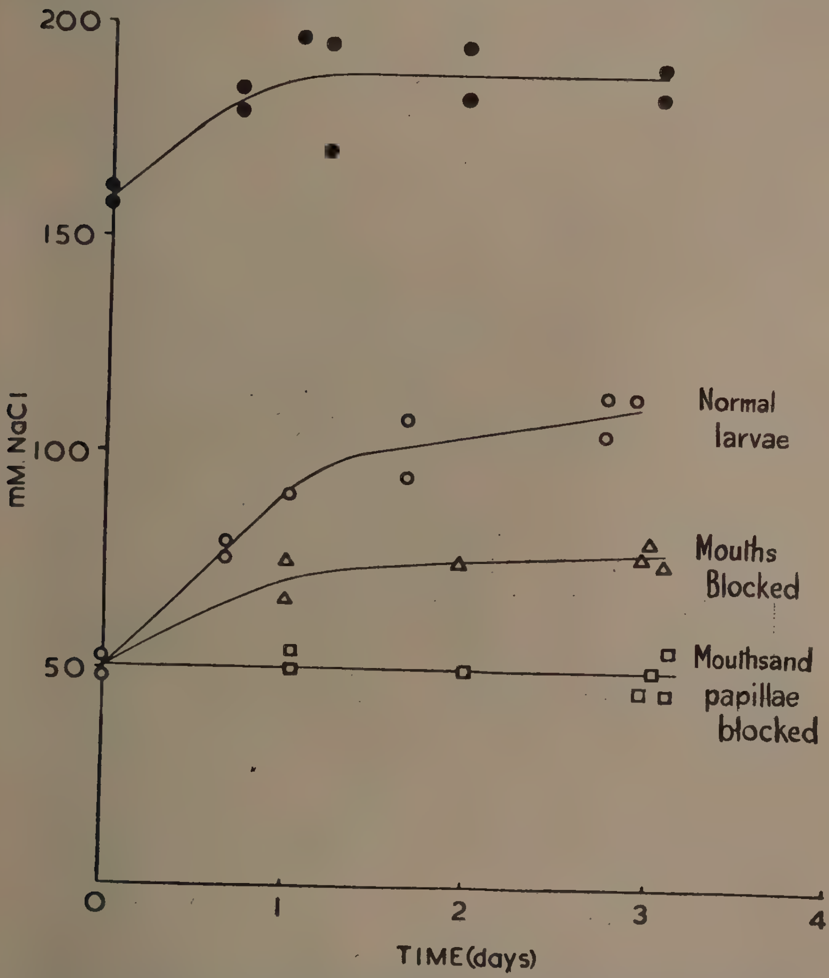

Fig. 4.—The effect of a 137 mM NaCl solution on the osmotic pressure of normal larvae (closed circles) and chloride concentration of normal and operated larvae (open symbols).

The total body chloride of freshly caught larvae was about 1·40 mg. Cl/gram tissue. When they were starved in glass distilled water at 15° C. the chloride content fell rapidly, for two days, to a value of approximately 0·90 and then more gradually to a value of about 0·85 after seven days. These results together with those for larvae starved in Failand stream water, are illustrated in fig. 5.

In order to determine whether an active ion absorbing mechanism exists in this species, larvae were washed for three days in glass distilled water, and then transferred to well aerated stream water, at 15° C. From fig. 6 it will be seen that there was a steady rise in the chloride content of larvae kept in stream water. The chloride content after five days in stream water was about 1·20 mg. Cl/gram tissue, which approximates to the chloride content of larvae which had been starved in stream water for seven days. Active absorption of chloride ions does, therefore, take place in this species.

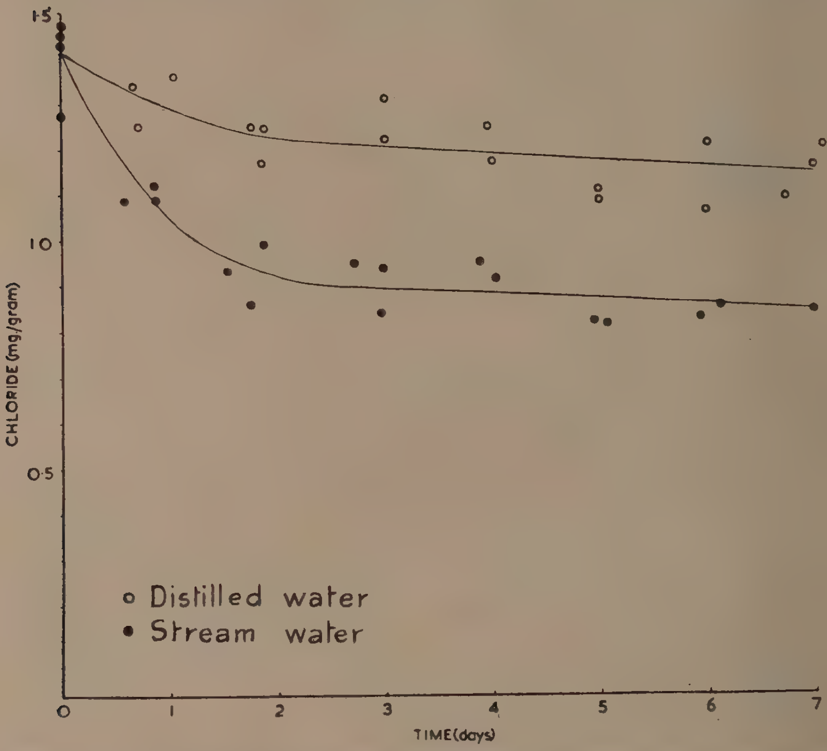

Fig. 5.—The effect of starvation in glass distilled water and Failand stream water on the total body chloride content of larvae of *H. marginata.*

To determine the site of absorption of chloride ions, the uptake was studied in larvae which had their mouths, and in some also the papillae, blocked with Whitehead's Varnish. Both lots of larvae were kept in well aerated stream water at 15° C. The chloride contents after four days, together with those for normal larvae kept under the same conditions, are given in Table II.

TABLE II.

Type of larva.	Weight (2 larvae). mg.	Cl. (mg./gram tissue).	Mean.
Normal	7·0	1·20	1·14
	8·5	1·12	
	9·2	1·11	
	9·3	1·12	
Mouth blocked	7·9	0·92	0·87
	9·4	0·87	
	8·4	0·81	
	9·8	0·89	
Mouth and papillae blocked	10·2	0·78	0·77
	12·3	0·73	
	10·2	0·79	

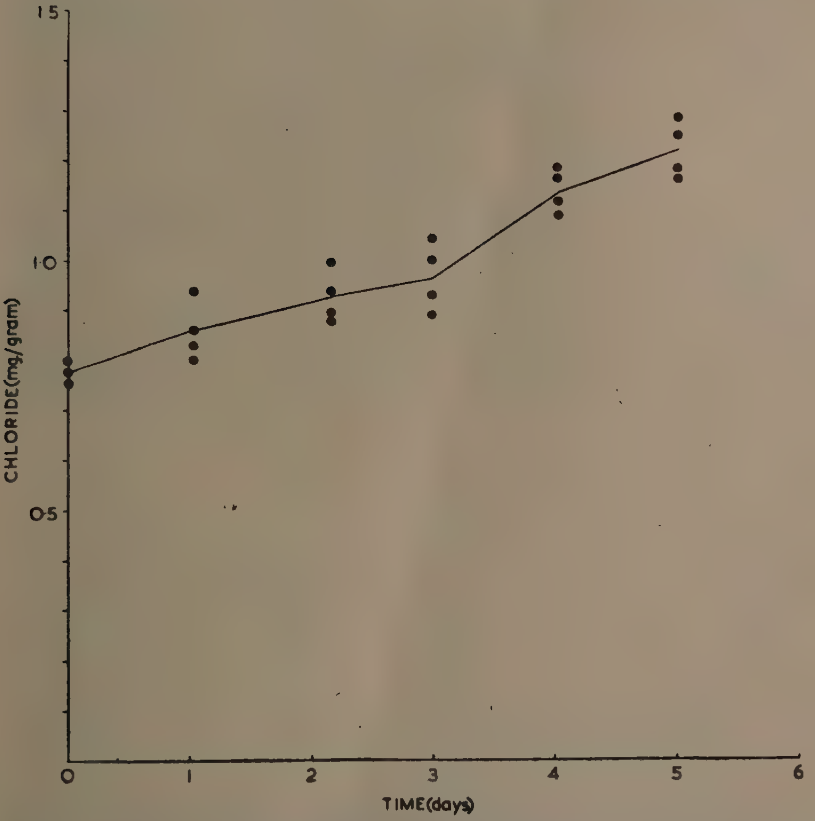

FIG. 6.—The uptake of chloride from stream water (0·35 mM NaCl) by larvae of *H. marginata* which had been washed in glass distilled water for three days.

The results indicate that a considerable amount of the chloride uptake takes place through the gut. There is a smaller difference between the chloride contents of larvae with their mouths blocked and those with mouths and papillae blocked. The results are, however, significantly different ($P = 0{\cdot}02 > 0{\cdot}01$), and some absorption does take place by the anal papillae.

These experiments were repeated, placing the larvae in a 15 mM NaCl solution, after washing for three days in glass distilled water. This concentration was similar to that of the haemolymph chloride of starved larvae, so that any

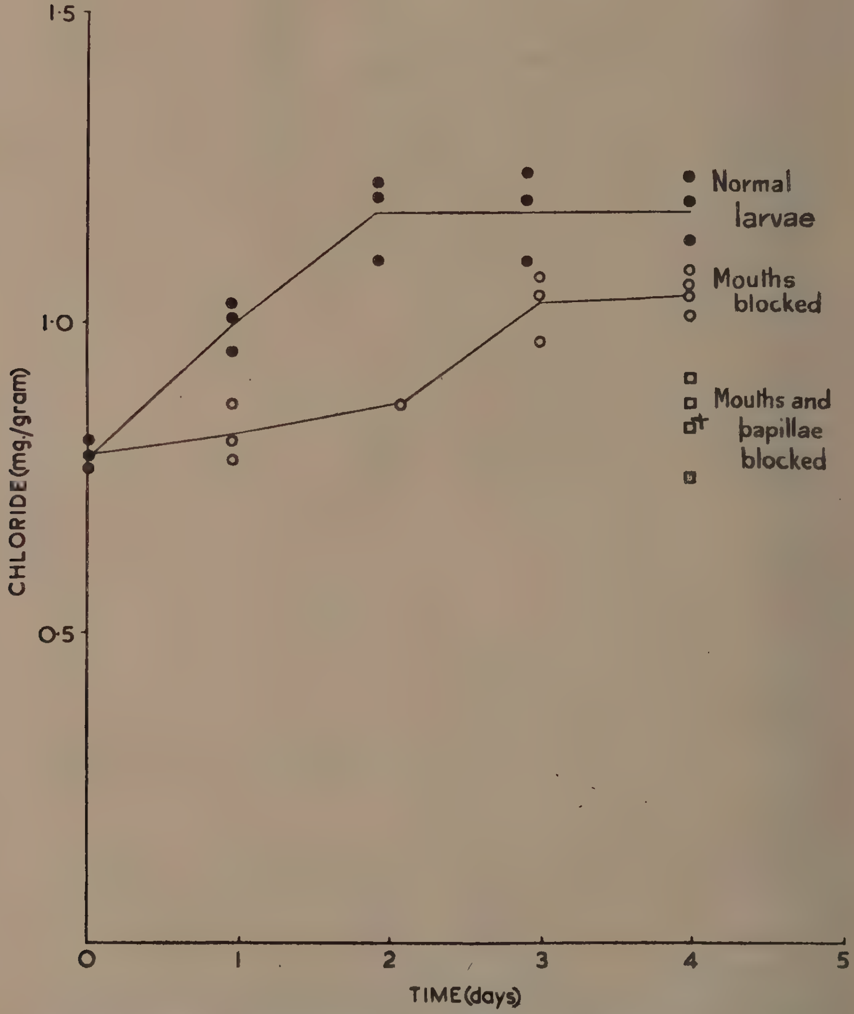

Fig. 7.—The uptake of chloride from a 15 mM NaCl solution by larvae of *H. marginata*, after being washed for three days in glass distilled water.

increase in the chloride content will involve an active absorption of this ion. It was hoped that by using a solution of this concentration it would be possible to demonstrate more clearly the part played by the anal papillae. With normal larvae there was a rise to a value of 1·18 mg. Cl./gram tissue within two days (fig. 7). The less rapid rise obtained in larvae which had their mounths blocked and the fact that there was no detectable increase in larvae which, in addition, had their papillae blocked, indicates that the anal papillae and the gut both play a part in chloride uptake.

It is possible that the increase in chloride content of normal larvae might be due, in part at least, to the presence of chlorides in the gut, and not necessarily to any active absorption into the haemolymph. If this were so it would be expected that larvae kept in a 15 mM NaCl solution would have a higher chloride content than those kept in stream water. This is not so however, and it seems reasonable to conclude that the presence of stream water in the gut does not affect the results to any serious extent. Also the volume of the gut, as judged by calculations made from measurements of the guts of larvae fed with Trypan Blue, is of the order of 0·103 cu.m.m. This is an outside estimate, and assuming the gut to be filled with stream water (13·2 μg. Cl/ml.) throughout the whole of its length, then the amount of chloride in the gut could not account for a rise of more than 0·0003 mg. Cl/gram tissue, which is within the experimental error of the method.

d. *Effect of Silver Nitrate on the Anal Papillae.*

Larvae of both species were placed in 1·0 and 0·1 mM solutions of silver nitrate, and left for two days in a darkened place. Some of the larvae in the 1·0 mM solution were dead after this time due to the toxic effects of the silver nitrate. The papillae were then exposed to light to reduce any absorbed silver to the black metallic silver. It was found that the papillae took up silver, showing a heavy black staining. Larvae kept in the 0·1 mM $AgNO_3$ solution showed stronger staining than larvae in the 1·0 mM solution. This must have been due to the more toxic effects of the more concentrated solution.

V. DISCUSSION.

It is clear from the results obtained that the larvae of both species of *Helodes* lose chloride ions fairly rapidly from the haemolymph when kept in distilled water. There is also a loss of chloride when the larvae were starved in stream water, the level in the haemolymph falling by half over a period of seven days. In this respect the larvae of *Helodes* would appear to be similar to *Aedes* and *Culex* (Wigglesworth, 1938), differing, therefore, from *Sialis* (Beadle and Shaw, 1950) in which the loss of chloride from the haemolymph is relatively slow. Koch (1938) suggests that the loss of chloride ions in *Chironomus* takes place mainly through the body surface of the larva. This clearly is not the case in *Helodes*, for larvae which had their mouths blocked showed only a barely detectable fall in chloride concentration and no change in osmotic pressure when starved in glass distilled water for four days. It seems probable that most of the chloride is lost in excretion of fluid by the Malpighian tubules. These results also indicate that the general body surface of the larva must be relatively impermeable to water, being similar to *Aedes* (Wigglesworth, 1933), *Eristalis* (Krogh, 1943), and *Corethra plumicornis* (Schaller, 1949).

It was shown that the body surface of *Helodes* is relatively impermeable to chloride against a concentration gradient, most of the chloride entering the haemolymph through the gut and anal papillae. Beadle (1939) showed that in the larva of *Aedes detritus* salt exchange occurred through the gut, which forms the most important permeable surface, the body surface and the small anal papillae being impermeable to salts and water.

In both species of *Helodes* the non-chloride fraction of the haemolymph can be regulated so that the total osmotic pressure of the haemolymph remains relatively constant. In dilute media the non-chloride fraction tends to increase, while in more concentrated media it becomes reduced, thus compensating for changes in the concentration of the haemolymph chloride. Regulation of the non-chloride fraction was first described by Wigglesworth (1938) in mosquito larvae, and since then it has been demonstrated in *A. detritus* (Beadle, 1939), *Sialis* (Beadle and Shaw, 1950) and in *Aeshna* and *Libellula* (Schoffeniels, 1950). It has been known for some time that in insects only a relatively small part of the total osmotic pressure is due to chlorides and that the amino-acids are probably the most important constituents (Duval, Portier and Courtois, 1928; Florkin,1937). More recently it has been shown that in the larva of *Aeshna cyanea* (Raper and Shaw, 1950) the relatively high non-protein content is due to a number of highly soluble amino-acids. Beadle and Shaw (1950) have clearly demonstrated that a compensatory regulation of the non-protein nitrogen takes place in the haemolymph of *Sialis*, and these authors suggest that changes in the non-protein nitrogen occur at the expense of the protein.

Larvae of *H. marginata*, which had been washed in running distilled water, were able to absorb chloride ions against a steep concentration gradient when returned to stream water. The uptake of chloride ions takes place chiefly through the gut and anal papillae. The ability of aquatic insects to absorb chloride ions from very dilute media was first demonstrated by Koch (1938) in *Culex* and *Chironomus*. It was shown conclusively that active absorption takes place exclusively through the anal papillae,which thus play an important part in maintaining the salt content of haemolymph. The papillae seem to have little significance as respiratory structures (Fox, 1920 ; Wigglesworth, 1933) and the larva of *H. minuta* would appear to be similar in this respect (Treherne, 1952). Recently Ramsay (1953) has demonstrated that the anal papillae of *A. aegypti* are capable of taking up sodium and potassium into the haemolymph against steep concentration gradients. Experiments using labelled sodium have shown that a smaller proportion also enters the haemolymph through the gut, the body surface being relatively impermeable to sodium (Treherne, 1954). *Helodes* differs, therefore, from these larvae of the Diptera in that the gut plays an important part in the uptake of chloride ions from the external medium. The larvae showed a steady loss of chloride when starved in stream water, which indicates that the active absorption process alone is not capable of maintaining a constant chloride level. Some of the loss must, therefore, be made good by salts contained in the food. By comparison with the results given by Koch (1938) the process of uptake of chloride ions by *Helodes* appears to be less efficient than in *Chironomus* and *Culex*. In the larva of *Sialis*, which seems to be the only other insect in which this process has been looked for, there is no active uptake of chloride ions from the external medium (Beadle and Shaw, 1950).

Koch (1934) found that the anal papillae of various larvae of the Diptera were able to absorb silver from very dilute solutions of silver nitrate, the metal becoming precipitated within the cells and later reduced under the influence of light to metallic silver. The anal papillae of *Helodes* behave in a similar way, the general body surface being unaffected. Krogh (1939) suggests that, as Na^+ and Ag^+ are chemically related, the Ag ion may be taken up by an Na absorbing mechanism. It should be borne in mind, however, that in the mosquite larva separate mechanisms appear to be responsible for the uptake of the closely related ions of sodium and potassium (Treherne, 1954).

VI. Acknowledgments.

I wish to thank Dr. H. E. Hinton, who supervised this work, for his advice and criticism. I am also indebted to Professor J. E. Harris for many helpful discussions. This work was carried out during the tenure of a grant from the Department of Scientific and Industrial Research.

VII. Summary.

1. The osmotic pressure of the haemolymph of the larva of *Helodes minuta* is equivalent to 155–171 mM NaCl, whilst that of *H. marginata* is equivalent to 154–167 mM NaCl. In both species chlorides account for about 30 per cent. of the total osmotic pressure.

2. During starvation in distilled water there is a fairly rapid loss of chloride ions from the haemolymph. The less rapid fall in osmotic pressure indicates that there is some regulation by the non-chloride fraction of the haemolymph.

3. The body surface is relatively impermeable to chloride against a concentration gradient, most of the chloride entering the haemolymph through the gut and anal papillae.

4. There is an active absorption of chloride ions from dilute media, both the gut and the anal papillae playing a part in this process. The papillae appear to have little significance as respiratory structures, and it is concluded that one of their main functions is the absorption of salts from the external medium.

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Vol. 105. Part 8. Pp. 131–150. 2 plates, 13 figs. 30th June, 1954

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OF
LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

Price 8s. 6d.

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A REVISION OF THE SPECIES OF *QUADRACEPS* (MALLOPHAGA) PARASITIC ON TRINGINAE.

By G. H. E. Hopkins, O.B.E., M.A., F.R.E.S.,

and

G. Timmermann, D.Sc.

Manuscript received 2nd September, 1953.
(Read 4th November, 1953.)

With 2 Plates and 13 Text-figures.

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Introduction.

General.

The older workers on Mallophaga neither understood the value of the male genitalia as specific criteria, nor possessed a medium for preserving their specimens in such a way that the genitalia could be effectively studied. It is, therefore, hardly surprising that many of their supposed species are actually composite, and that many of their host-records are erroneous, but it is a good deal more surprising that the errors still persist even after Waterston (1914 : 479 ; 1915 : 171–176), following Mjöberg's lead, had pointed out the importance of the male genitalia and had published good figures of a number of species. Yet in a recent book on Mallophaga and other arthropod parasites, a species of *Quadraceps* that is almost certainly monoxenous (i.e., occurring on only one species of host) is alleged to occur on no less than 13 different species of Charadriiformes, some of which are not even at all closely related to its true host.

The fact that the Halle collection of Mallophaga, containing the type-material of all species described by Nitzsch, Burmeister and Giebel, was almost completely destroyed during the 1939–45 war means that for the interpretation of the older names we are often dependent on an inadequate description of a composite "species." In these circumstances the degree to which the species of host can be relied upon for aid in the identification of the parasites is of much importance. During the preparation of this paper, and another on the *Quadraceps* of Vanellinae which will be published by G. T., excluding specimens collected by techniques that are known to be conducive to contamination (from bird-skins in museums, for instance), and instances in which we do not know what technique was employed, we have examined batches of *Quadraceps* from 106 individuals of a dozen species of Tringinae and Vanellinae, and in only one instance have we encountered a species of *Quadraceps* on a host to which it is not normal. The single exception is most instructive: a tube of parasites from *Tringa glareola* proved to contain a mixture of *Quadraceps obscurus* (Burm.) and *Q. quadrisetaceus* (Piaget), the former predominating; investigation of other material from the same source soon revealed a tube from *Rostratula benghalensis* collected at the same place on the same day, and the proof that the presence of *Q. quadrisetaceus* on *T. glareola* was due to post-mortem contamination was complete when the tube from *Rostratula* was found to contain a mixture of the same two species of *Quadraceps* with *Q. quadrisetaceus* predominating. It may, therefore, safely be stated that straggling, at least in this section of the genus, is a rare phenomenon, and that the host-records are a good indication of parasite-species.

In the present paper we revise the *Quadraceps* of Tringinae, laying particular stress on the characters of the male genitalia. We also comment on the indications as to the relationships of the hosts furnished by the parasites, but in considering our remarks on this subject it is important to remember that they are based on only one species of Ischnocera from each host-species, and that therefore the possibility of secondary infestation cannot be excluded though we have no reason to assume that it has occurred.

All holotypes, allotypes and neotypes erected in this paper are in the British Museum (Natural History).

All the descriptions and figures are from specimens which have been cleared and mounted in Canada balsam, which inevitably involves some distortion, and especially some flattening of the abdomen. Unless otherwise stated, all the descriptions and figures of genitalia are taken from specimens of which the genitalia have been dissected out and mounted separately. This is a point of considerable importance, because in some instances the appearance of the genitalia when *in situ* is greatly affected by foreshortening.

For names of birds we have, unless otherwise stated, followed Peters (1934), regardless of whether we agree with his arrangement.

Acknowledgments.

We owe a great deal of the Uganda material to Drs. W. J. Eggeling and A. W. Williams and Messrs. T. W. Chorley, the late G. L. R. Hancock and R. G. Sangster; the collections from Tanganyika Territory were mostly made by Mr. H. F. I. Elliott. The South African material was nearly all obtained from skins preserved in the Transvaal Museum, Pretoria, by G. H. E. H., who is deeply indebted to the late Dr. Austen Roberts for permission to examine these skins. We are indebted to the Trustees of the British Museum for the opportunity to examine the Mallophaga in the Museum, particularly the Denny, Piaget and Meinertzhagen collections. Other important material has been made available by Messrs. M. A. Carriker and L. R. Guimarães.

Dr. Waterston was apparently making preparations for a revision of *Quadraceps* and related genera when he died, for a number of drawings had been prepared for him by Mr. Engel Terzi (Clay and Meinertzhagen, 1939 : 450). These drawings (figs. 3, 6–8, 10 and 11) have been kindly placed at our disposal by the Trustees of the British Museum, to whom we are also indebted for all the photographs. These drawings have been supplemented by others (figs. 5, 9, 12 and 13) very kindly contributed by Mr. F. G. A. M. Smit; figs. 1 and 2 have been kindly made available by Col. R. Meinertzhagen, and fig. 4 is by G. T.

We are particularly grateful to Miss Theresa Clay for reading and criticising large portions of the manuscript and for helping us in many other ways.

QUADRACEPS CLAY AND MEINERTZHAGEN, 1939.

Quadraceps Clay and Meinertzhagen, 1939, *Ann. Mag. nat. Hist.* (11) **4** : 453. Type species: *Degeeriella vanelli* (Denny).

Koeniginirmus Eichler, 1940, *Zool. Anz.* **130** : 101. Type species: "*Koeniginirmus punctatus* (Nitzsch in Burmeister, 1838, jedoch sensu A. Koenig)."

Oedicnemiceps Eichler, 1943, *Zool. Anz.* **141** : 59. Type species: "*Docophorus antennatus* N.i.D. sensu Piaget, 1880, a p. 664; pl. LIV, f. 5."

Glareolites Eichler, 1944, *Stettin. ent. Ztg* **105** : 80. Type species: *Nirmus ellipticus* Nitzsch.

Mjöberginirmus Eichler, 1944, *Stettin. ent. Ztg* **105** : 85. Type species: *Nirmus obliquus* Mjöberg.

Nirmoides Eichler, 1944, *Stettin. ent. Ztg* **105** : 81. Type species: *Docophorus antennatus* Piaget.

Szidatiella Eichler, 1944, *Stettin. ent. Ztg* **105** : 81. Type species: *Docophorus elongatus* Piaget.

Haematophagus Timmermann, 1950, *Fauna islandica,* no. **2** : 1, 2. Type species: *Quadraceps haematopi* (Denny).

Head with broad hyaline margin arising from near anterior end of premarginal carina; premarginal and ventral carinae fused near their anterior ends but the actual tips free. Dorsal carina on each side passing inwards to form a narrow median suture. A narrow postantennal suture each side, transverse carina and temporal carinae (as in *Carduiceps*) present in some species. Pterothorax with lateral margins divergent. Abdomen with segment I small; paratergal plates with elongated re-entrant "heads" but without inwardly directed processes; tergal plates of some or all segments partly or completely divided in the median line. Apparent segment IX in male clearly demarcated from apparent segment VIII.

The male genitalia are of a complicated type not at all unlike that found in *Saemundssonia* (see Waterston, 1915 : 22, figs. A, B), which we agree with Waterston in considering to be probably primitive. The basal plate, parameres and penis are much as in *Saemundssonia,* though the penis may (as in *Q. furvus*) be much more developed; the endomeres are far more developed in *Quadraceps* and the telomeres are normally fused and may form a tube enclosing the penis; the hypomere, beneath the base of the penis, is (as Waterston notes) very difficult to distinguish.

The genus is separable from *Lunaceps* and *Carduiceps* by the fact that the hyaline margin arises anterior to the dorsal preantennal suture and by the posterior prolongation of this suture in the median line. Hopkins (1949 : 34) suggested that the existence of nirmoid species of *Cummingsiella* like *C. ambigua* (Burm.) made it improbable that *Quadraceps* could be separated from *Cummingsiella,* but Miss Clay kindly informs us that in the former genus (as in *Saemundssonia*) the temporal carina is separated from the postmarginal carina by the postantennal suture, whereas in *Cummingsiella* the two carinae meet. It seems possible that *Quadraceps* is more closely related to *Saemundssonia* than to the nirmoid species of *Cummingsiella* which are superficially so similar, and the fact that nirmoid and docophoroid forms have evidently diverged from a common stock on at least two separate occasions within this group of genera is of considerable interest.

Quadraceps contains a number of fairly distinct natural groups, to most of which generic rank has been given. The most distinct of the larger groups is *Koeniginirmus* Eichler, and the type species of this genus is admittedly superficially very different from the type species of *Quadraceps* (*Q. hospes* (Nitzsch), 1866, of which *Q. vanelli* (Denny), 1842, *nec Q. vanelli* (Schrank), 1803, is a synonym). The essential characters, however, are the same and there is an almost perfect transition from one type to the other through *Q. sellatus* (Burm.), *Q. felix* (Giebel), *Q. eugrammicus* (Burm.), *Q. birostris* (Giebel) and *Q. separatus* (Kellogg and Kuwana), all of which are from gulls or terns and would have to be included in *Koeniginirmus* if the group is recognised. We consider all of the names given by Eichler to be synonyms of *Quadraceps* and not even worthy of retention as subgenera.

The distribution of the genus is imperfectly known but appears to be very peculiar. It certainly occurs on all three of the groups (Charadrii, Lari and Alcae) treated by Peters as suborders of the Charadriiformes, and is present on all the larger families. But its distribution on the Scolopacidae is sporadic, since it seems not to occur on *Limosa* and *Numenius*, the Scolopacinae and the Eroliinae, being replaced on at least most members of these groups by *Lunaceps*, *Rhynonirmus* and *Carduiceps*. There are undoubted instances of the normal occurrence of two species of the genus on the same host-species and even on the same individual, but they appear to be decidedly rare.

The *Quadraceps*-species of the Tringinae.

The species of *Quadraceps* found on this group of avian hosts are of very uniform structure (figs. 1, 2). Without exception they are moderately slender forms, fulvous to dark brown in colour, and with more or less advanced division of the otherwise-continuous transverse abdominal dorsal plates or tergites, of which that of the apparent seventh segment (that bearing the last spiracular opening) in the male of all species is strongly narrowed and divided in the median line. The chaetotaxy of the body of all the species is in extensive general agreement and represents a type, as is also the case in other groups of the great " nirmoid " complex of genera.

The male genitalia, on the other hand, are extremely distinctive and fall into a number of different types ; in consequence they are of the first importance as taxonomic criteria for the separation of the individual species.

We may also emphasise that in general every member of the Tringinae is parasitised by its own characteristic *Quadraceps*, though we have found two instances in which we are unable to separate the forms found on two Tringinae regarded by ornithologists as specifically distinct, and that there is only one instance in which we think that two forms could reasonably be placed as subspecies of a polytypic species. This marked separation of the individual forms from one another may mean that the *Quadraceps*-species of the Tringinae (and hence their hosts) are phylogenetically ancient forms which already have a long evolution behind them.

Quadraceps obscurus (Burmeister), 1838.

(Figs. 1–4; Pl. I, figs. 1, 2.)

Type host: *Tringa glareola* Linn.

Nirmus obscurus Burmeister, 1838, *Handbuch Ent.* **2** : 427 (in part).
Nirmus obscurus N. Giebel, 1866, *Z. ges. NatWiss.* **28** : 374 (in part).
Nirmus obscurus Nitzsch ; Giebel, 1874, *Insecta epizoa* : 163, pl. 6, figs. 2, 3 (in part).
Nirmus obscurus Giebel ; Piaget, 1880, *Les Pédiculines* : 170 (wrongly placed as a synonym of *N. furvus*).
Degeeriella obscura Burmeister ; Harrison, 1916, *Parasitology*, **9** : 119.
Quadraceps obscurus (Burmeister) ; Hopkins, 1942, *Ann. Mag. nat. Hist.* (11) **9** : 115.
Degeeriella obscura (Nitzsch) ; Blagoveshtchensky, 1948, *Mag. Parasit., Leningr.* **10** : 283, figs. 16, 16*a*.

The hosts mentioned in the very brief original description are " Totan. glareola, Tot. hypol. und Limos. melanura." We accept as a principle that the first host mentioned by an author should be regarded as the type host in the absence of strong contraindications (an important restriction of the principle that is too often ignored) and in this instance material from this host agrees with the description ; we therefore regard *Tringa glareola* as the type host. The two descriptions of the species published by Giebel both refer to the same material as was employed by Burmeister and contain the same list of hosts. Piaget considered the species inseparable from *furvus*, but apparently without having seen it, for the portion of his collection in the British Museum contains no specimens of *obscurus*. From the lists of hosts given by Denny and by Mjöberg it is evident that the material they described as *Nirmus obscurus* was not this species. Other authors subsequent to Piaget have mostly accepted his opinion, but Harrison and Hopkins each listed *obscurus* as a good species with *Tringa glareola* as its type host, and Blagoveshtchensky's figures show clearly that the species he described is the correct one. The type-material of the species, like that of all other species in the genus *Quadraceps* described by Nitzsch, Burmeister and Giebel, was lost in the almost complete destruction of Nitzsch's collection during the 1939–1945 war.

A narrow species. Lateral outlines of clypeus straight.

Male (Pl. I, fig. 1).—Dark-coloured,[1] paratergal plates nearly black, tergal and sternal plates rather dark brown and covering almost entire dorsal and ventral surfaces of abdomen. Length 1·68–1·80 mm.

Dorsal anterior plate of head (" signature ") shield-shaped, its posterior angle fairly well marked. Median posterior angle of pterothorax very obtuse and not well marked, latero-posterior angles with one very small and one long seta followed by a group of 3 rather long setae. Posterior margin of pterothorax (from outer end to middle) with 1 very long, 1 shorter and 1 still smaller seta on each side. Abdomen 3·0–3·1 times as long as wide, widest at fourth or fifth segment, its sides very weakly convex. First abdominal

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[1] Many of the Mallophaga in the Hopkins collection were cleared by boiling in a solution of caustic potash and are consequently partly decolourised. Our notes on colour have usually been taken from material preserved in alcohol.

tergite completely divided in the median line,[2] second and third with incision extending almost to posterior margin, fourth sometimes very deeply and more frequently quite shallowly incised, fifth and sixth at most shallowly notched, seventh divided, eighth not divided but with a posterior median incision reaching about to the middle, terminal tergite well-separated, crescentic with rounded apices, its concave anterior margin not lobed. First tergite with on each side a single tergocentral seta,[3] second to fifth with 2, sixth with 1, all these setae slender or very slender and much shorter than the segments from which they arise; a single stout and very long tergolateral seta on segments 3–6 and a much smaller one on segment 7. Paratergites only slightly oblique to long axis of abdomen, narrow; pleural setae slender and of moderate length. Gular and pterothoracic sternal plates well developed, former with its anterior portion an equilateral triangle with almost straight sides and its posterior portion roughly quadrangular, slightly broader than long, and containing a quadrangular pale area which is longer than broad, pterothoracic plate

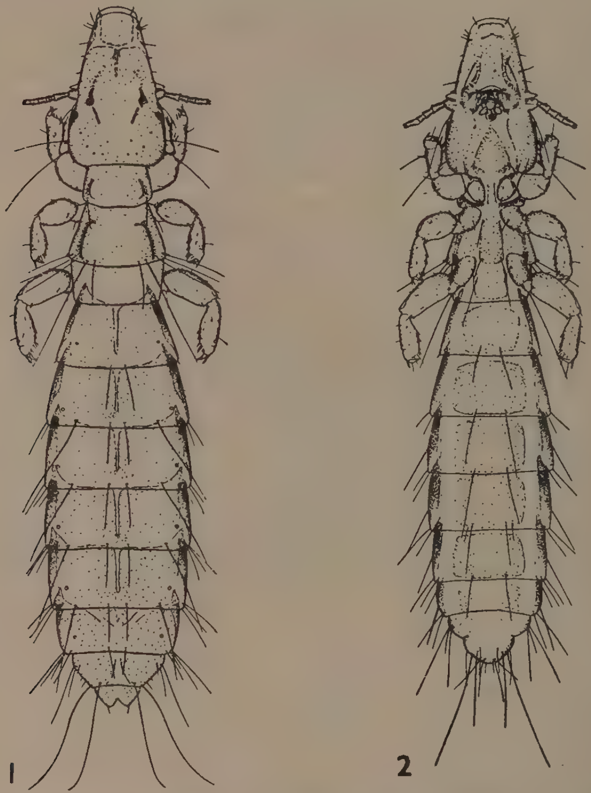

Fig. 1–2.—*Q. obscurus* (Burmeister). (1) Dorsal surface of female. (2) Ventral surface of male.

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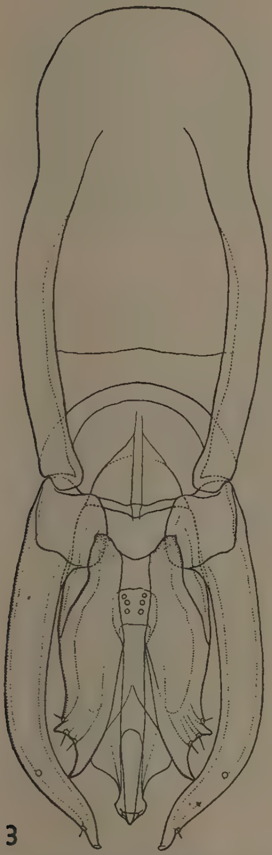
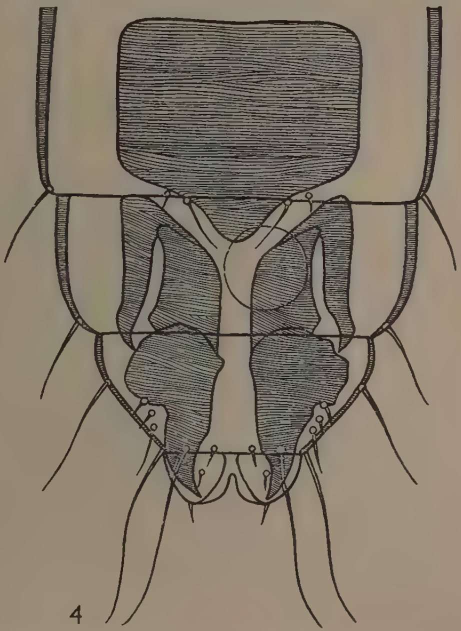
[2] Our numbering of segments applies solely to the apparent segments, and the word "apparent" should be understood before the number in every instance.

[3] For the nomenclature of setae see Kéler, 1938, *Nova Acta Leopoldina* (N.F.) **5** : 419.

elongate oval with a single small anterior lateral seta and a similar posterior lateral seta. Sternite of first abdominal segment roughly bell-shaped and bearing on each side a single sternocentral seta slightly longer than the plate itself, sternites of remaining segments quadrangular.

Genitalia (fig. 3): basal plate moderately long, with a conspicuous median basal splint. Parameres rather long and slender, tapering slightly and gradually, regularly curved inwards from base to about three-quarters, then more strongly curved, extreme tips curved outwards; endomeres very stout and rather long (five-eighths length of parameres), outer aspect with a large and prominent triangular tooth with serrated tip at about eleven-thirteenths, apex curved outwards in the shape of a rose-thorn with moderately sharp tip; penis straight, projecting very little beyond the hypomere.





Figs. 3–4.—*Q. obscurus* (Burmeister). (3) Genitalia of male from *Tringa stagnatilis* near Le Havre, France. (4) Ventral surface of terminal segments of abdomen of of female from *Tringa glareola*.

Female (Pl. I, fig. 2).—Only slightly paler than male. Length 1·9–2·0 mm. Abdomen 3·1–3·3 times as long as wide, very narrow at first segment, widest at fourth and fifth, its sides only slightly convex. First tergal plate completely divided, second to sixth incised almost to posterior margin (sixth rarely hardly beyond half), seventh and eighth usually shallowly notched. Terminal segment bilobed, the lobes with smoothly rounded apices and divided by a shallow sulcus. Ventral surface of terminal segments as in fig. 4.

Neotype a male (Pl. I, fig. 1) and *neallotype* a female (Pl. I, fig. 2) from *Tringa glareola* Linn., KENYA: Nanyuki, –.iii.1949, Meinertzhagen coll. no. 18830.

Other material examined.—67 male and 72 female neoparatypes from *Tringa glareola*, Kenya, Uganda, Sudan, South Africa, Germany, Czechoslovakia, Estonia and England. Specimens from *Tringa stagnatilis* (Bechstein), of which we have examined 47 males and 30 females from Kenya, Uganda, Sudan, India, Iran and France, appear to be inseparable from those from the type host. Blagoveshtchensky gives drawings of the genitalia of a male from *Tringa glareola* and one from *Tringa stagnatilis* as his figs. 16 and 16*a* respectively, but the slight differences he depicts seem to be within the range of individual variation.

Quadraceps falcigerus (Peters), 1951.
(Fig. 5; Pl. I, figs. 3, 4.)

Type host: *Tringa flavipes* Gmelin.

Degeeriella falcigera; Peters, 1931, *Ann. ent. Soc. Amer.* **24**: 583, fig. 1.
Quadraceps falcigerus (Peters); Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga*: 310.

Described from a very long series collected from *Totanus flavipes* (Gmelin) (now known as *Tringa flavipes*) from Sandusky, Ohio (type locality) and other localities in the United States and the Bahama Islands.

Darker than *Q. obscurus*, in particular the paratergites blacker and more extensive. The principal difference, however, is in the structure of the male genitalia (fig. 5), which resemble those of *Q. obscurus* in general (in the shape of the parameres, for instance) but differ in many details: basal plate narrower and with straighter margins; tips of parameres slightly more curved outwards; endomeres with lateral tooth much larger, placed nearer base (its centre at about two-thirds), and forming an equilateral triangle decidedly reminiscent of the lateral fin of a skate, or ray, apex of endomere also longer than in *obscurus*; penis and telomere subequal in length, not nearly reaching level of apex of endomere; telomere narrower and without the pronounced preapical outward bulge found in *obscurus*.

The resemblance to *Q. obscurus* is sufficient to suggest that the two species are more closely related to one another than are any other pair of species found on the Tringinae. But the differences in the male genitalia seem too great to allow of *Q. falcigerus* and *Q. obscurus* being considered to be conspecific[4]

Holotype male and *allotype* female, United States National Museum cat. no. 43514 (not seen).

Material examined.—The 17 males and 11 females of *Q. falcigerus* that we have examined are all from *Tringa flavipes* Gmelin, and include a pair of paratypes. They are from U.S.A., Canada and Brazil.

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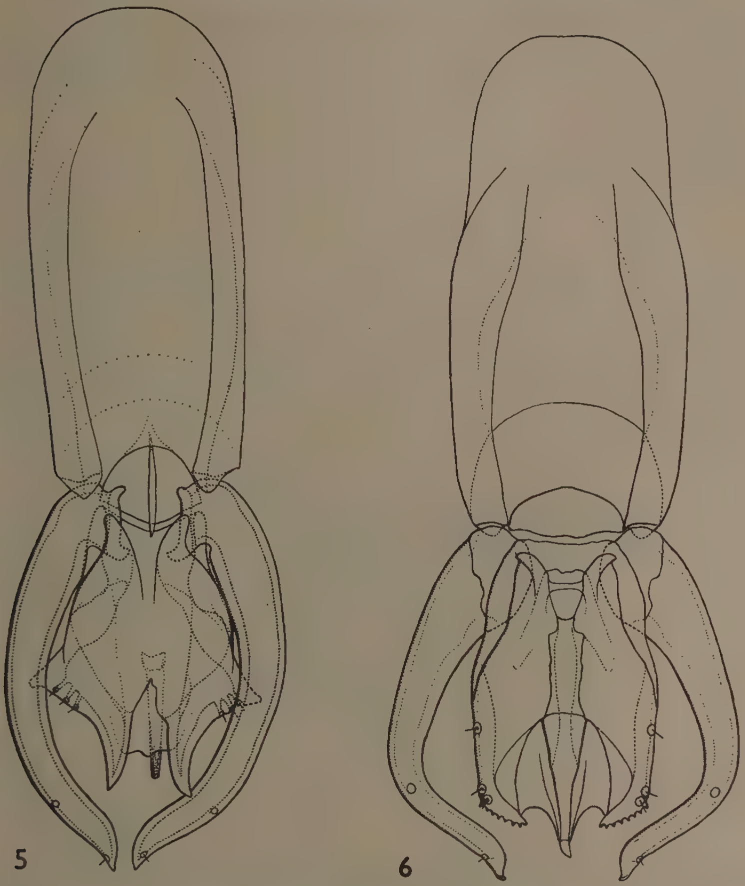
[4] G. T. does not agree and would prefer to consider *falcigerus* a subspecies of *obscurus*.



Figs. 5–6.—(5) *Q. falcigerus* (Peters). Genitalia of a male paratype. (6) *Q. similis* (Giebel). Genitalia of male from *Tringa nebularia*, Avret Hissar, Greece.

Quadraceps similis (Giebel), 1866.
(Fig. 6 ; Pl. I, figs. 5, 6.)

Type host : *Tringa nebularia* (Gunnerus).

Nirmus similis ; Giebel, 1866, *Z. ges. NatWiss.* **28** : 374.
Nirmus similis Giebel ; Giebel, 1874, *Insecta epizoa* : 164.
Nirmus similis Giebel ; Piaget, 1880, *Les Pédiculines* : 170 (wrongly considered a synonym of *furvus*).
Nirmus interruptus ; Piaget, 1880, *l.c.* : 173, pl. 14, fig. 6.
Nirmus interruptus [Piaget] ; Piaget, 1885, *Pédiculines Supplément* : 21.
Nirmus interruptus Piaget ; Waterston, 1913, *Ent. mon. Mag.* **49** : 18.
Nirmus clypeatus ; Kellogg and Paine, 1914, *Rec. Indian Mus.* **10** : 237, pl. 14, fig. 3.
Degeeriella clypeata Kellogg and Paine ; Harrison, 1916, *Parasitology* **9** : 110.
Degeeriella interrupta Piaget ; Harrison, 1916, *l.c.* : 115.
Degeeriella similis Giebel ; Harrison, 1916, *l.c.* : 123.

Degeeriella austini; Peters, 1931, *Ann. ent. Soc. Amer.* **24**: 585, fig. 2.
Quadraceps similis (Giebel); Hopkins, 1942, *Ann. Mag. nat. Hist.* (11) **9**: 115.
Degeeriella dissimilis; Blagoveshtchensky, 1948, *Mag. Parasit., Leningr.* **10**: 283, figs. 15, 15*a*.
Quadraceps austini (Peters); Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga*: 309.
Quadraceps clypeatus (Kellogg and Paine); Hopkins and Clay, *l.c.*: 309.
Quadraceps similis (Giebel); Hopkins and Clay, 1952, *l.c.*: 316 (*interruptus* and *dissimilis* placed as synonyms).

Described from a single female obtained from *Totanus glottis*, now known as *Tringa nebularia* (Gunnerus). Piaget (1880: 170) seems to have sunk *similis* to *furvus* without having seen specimens, for, though he mentions *Totanus glottis* as a host, there are no specimens labelled *furvus* from this host in the portion of his collection which is in the British Museum. Piaget found on a skin of a cormorant, however, a *Quadraceps* which he described as *Nirmus interruptus* and which he subsequently recorded (1885: 21) from *Totanus glottis*; Waterston (1913) suggested that the true host of *interruptus* is *Tringa nebularia*, but apparently did not suspect its identity with *similis*. We have examined the male holotype of *interruptus* and one of the specimens that Piaget recorded as this species in 1885, and both are undoubtedly *similis*. Subsequent authors mostly accepted Piaget's erroneous belief that *similis* is indistinguishable from *furvus*. *Nirmus clypeatus* was described from a single male collected from a skin of *Corvus cornix*, Kashgar, E. Turkestan; we have been fortunate enough to have the opportunity to see the holotype (which belongs to the Indian Museum) and to confirm that it is *similis*; in view of the locality the true host must have been *Tringa nebularia*. *Degeeriella austini* Peters was described from specimens obtained from *Totanus melanoleucus* (now *Tringa melanoleuca*) from Windy Tickle, Labrador, while *D. dissimilis* Blagoveshtchensky is from *Tringa nebularia*.

Extremely similar to *Q. obscurus* but larger and darker. Lateral margins of clypeus straight.

Male (Pl. I, fig. 5).—Length 1·75–2·14 mm. First abdominal tergite not always wholly divided but very frequently only with a wedge-shaped incision reaching to the level of the alveoli of the median bristles, incisions of tergites 4–6 deeper, seventh and eighth tergites divided. Abdomen 2·9–3·0 times as long as broad.

Genitalia (fig. 6): Parameres long and slender, little tapered, very strongly bent at about two-thirds. Endomeres very broad, almost as long as penis and bound up with it, their apices obliquely truncate, finely but very distinctly serrate.

Female (Pl. I, fig. 6).—Similar to the same sex of *Q. obscurus* but larger (2·09–2·21 mm.). Abdomen 2·8–3·0 times as long as wide.

We are unable to separate specimens from *Tringa melanoleuca* from those from *T. nebularia*, though there is a small average difference in the male genitalia, the penis and telomeres usually (but not always) being shorter in the former, rarely extending beyond the endomeres. In view of the overlap, we think this average difference too small to permit of the recognition of *Q. austini* as a subspecies of *Q. similis*.

Neotype male and *neallotype* female from *Tringa nebularia* (Gunnerus), UGANDA: Bunyoro, Kibero, 31.xii.1933 (W. J. Eggeling).

Other material examined.—34 male and 42 female neoparatypes from *Tringa nebularia*, Uganda, South Africa, Aden, Britain and Greece. The male lectotype of *Nirmus interruptus* Piaget and the male holotype of *N. clypeatus* Kellogg and Paine. 15 males and 8 females from *Tringa melanoleuca* (Gmelin), U.S.A. and Brazil.

Quadraceps furvus (Burmeister), 1838.

(Fig. 7 ; Pl. I, figs. 7, 8.)

Type host : *Tringa erythropus* (Pallas).

Nirmus furvus ; Burmeister, 1838, *Handb. Ent.* **2** : 427 (in part).
Nirmus furvus ; Giebel, 1861, *Z. ges. NatWiss.* **18** : 312 (in part).
Nirmus furvus N. ; Giebel, 1866, *Z. ges. NatWiss.* **28** : 374 (in part).
Nirmus furvus Nitzsch ; Giebel, 1874, *Insecta epizoa* : 163, pl. 5, figs. 2, 3 (in part).
Nirmus furvus N. ; Piaget, 1880, *Pédiculines* : 169, pl. 14, fig. 3 (in part).
Degeeriella furva Nitzsch ; Harrison, 1916, *Parasitology* **9** : 113 (in part).
Quadraceps furvus (Burmeister) ; Hopkins, 1942, *Ann. Mag. nat. Hist.* (11) **9** : 115.
Degeeriella furva (Nitzsch) ; Blagoveshtchensky, 1948, *Mag. Parasit. Leningr. & Moscow*, **10** : 281, figs. 14, 14*a*.
Quadraceps furvus (Burmeister) ; Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga* : 311.

The very brief original description gives " Tot. maculat., T. glottis und Strepsil. interpres " as hosts, but agrees best with material from the first-named now known as *Tringa erythropus*. Giebel's main description, the figures and the Latin diagnosis quoted from Nitzsch's manuscript (Giebel, 1874 : 163) also seem to refer to material from this host. Piaget's redescription is partly from material from *Totanus fuscus* (= *Tringa erythropus*), but it is certain that he confused other species with *furvus*, for the material labelled by him with this name in the part of his collection that is in the British Museum comprises a single female of *furvus* and a series of 2 males and 6 females from *Vanellus cristatus* (now *V. vanellus*) ; the latter specimens, including one pair labelled both *furvus* and *obscurus*, are all *Quadraceps junceus* (Scopoli). Subsequent authors have described or recorded species of *Quadraceps* under the name *furvus*, but only Blagoveshtchensky appears to have had the species to which we restrict the name.

A somewhat compact species with straight lateral outlines of the clypeus. The specimens we have seen are yellowish brown, but all are mounted and may be somewhat decolorised.

Male (Pl. I, fig. 7).—Length 1·54–1·73 mm. First abdominal tergite divided, second to fifth deeply incised, sixth with shallow incision, seventh and eighth divided. Abdomen about 2·4 times as long as broad.

Genitalia (fig. 7) : Basal plate straight-sided, about twice as long as wide. Parameres long and slender, with a slight sigmoid curve, their outer margin notched just before the apex and there bearing a minute seta. Endomeres hardly more than half length of parameres, shaped like a very broad sabre-blade. Telomeres usually extending well beyond apex of endomeres, terminating in a blunt tip with two distinct laterally-directed teeth. Penis extremely characteristic, far longer than in any other species known to us, in mounted specimens extremely strongly curved into an S-shape and then bearing a marked resemblance to the trunk of an elephant with the bulbous base of the penis representing the forehead, but doubtless in unmounted specimens not bent over to one side but lying with the middle portion of its length vertical and directed towards the dorsum of the insect, when it would appear straight ; Blagoveschtchensky's fig. 14*a* seems to represent such a specimen.

Female (Pl. I, fig. 8).—First tergite completely divided, second to sixth deeply incised. Length 1·87–1·92 mm., abdomen 2·6 times as long as wide.

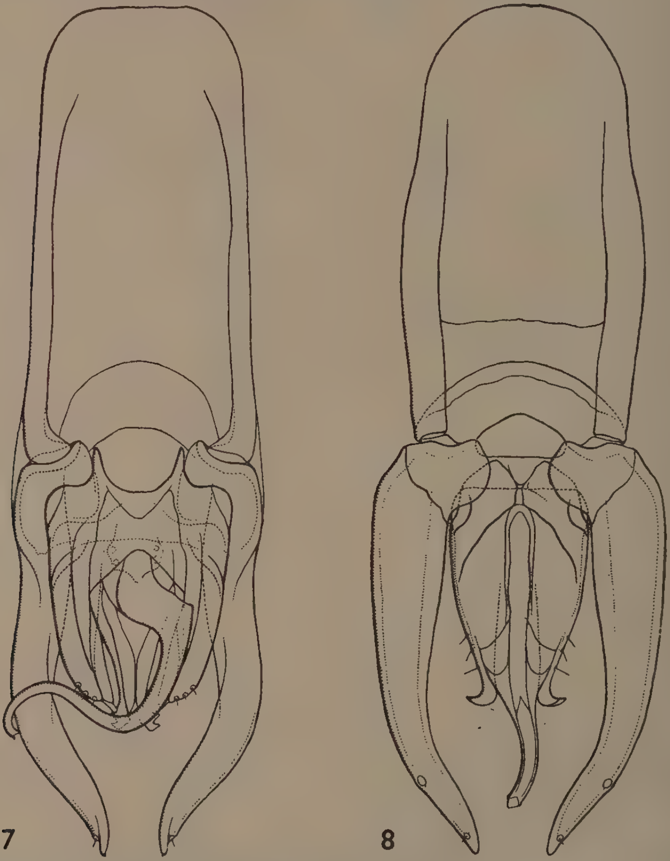
Type-material.—The original type-series was destroyed in the 1939–1945 war. We select as neotype a male (Pl. I, fig. 7) and as neallotype a female (Pl. I, fig. 8) from *Tringa erythropus* (Pallas), INDIA : Rajputana, –.i.1952, Meinertzhagen coll. no. 19617. We have also seen 24 male and 12 female neoparatypes from the same host-species, India, Japan, England and Lapland.

Quadraceps ochropi (Denny), 1842.

(Fig. 8 ; Pl. I, figs. 9, 10.)

Type host : *Tringa ochropus* Linn.

Nirmus ochropi ; Denny, 1842, *Mon. Anopl. Brit.* : 52, 134, pl. 11, fig. 12.
Nirmus ochropi Denny ; Piaget, 1880, *Pédiculines* : 170.
Degeeriella ochropi Denny ; Harrison, 1916, *Parasitology*, 9 : 119.



FIGS. 7–8.—(7) *Q. furvus* (Burmeister). Genitalia of male from *Tringa erythropus*, Yarmouth, England. (8) *Q. ochropi* (Denny). Genitalia of male from *Tringa ochropus*, Fair Isle, Shetland.

Quadraceps ochropi (Denny); Hopkins, 1942, *Ann. Mag. nat. Hist.* (11) **9**: 115.
Degeeriella ochropi (Denny); Blagoveshtchensky, 1948, *Mag. Parasit., Leningr. & Moscow,* **10**: 284, fig. 17.
Quadraceps ochropi (Denny); Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga*: 314.

Described from material of both sexes obtained from *Totanus ochropus* (now *Tringa ochropus*) in Britain; only one female of the type-series survives and this is not in good condition, having apparently been subjected to too much potash while being mounted. Piaget, evidently without having seen specimens, considered *ochropi* to be the same as *furvus*, but Harrison listed it as a good species.

A moderately narrow, rather dark brown species. Lateral margins of clypeus weakly concave.

Male (Pl. I, fig. 9).—Length 1·53–1·63 mm. Tergal plate of first abdominal segment medially divided or deeply incised, that of second deeply incised and that of third incised to beyond middle, plates of following segments slightly notched, that of seventh segment divided, that of eighth sometimes divided and sometimes merely with deep median anterior or posterior incision. Abdomen 2·7–2·9 times as long as wide.

Genitalia (fig. 8): Basal plate short, with well-developed transverse sclerotic bar but the median splint poorly developed. Parameres long, moderately stout and regularly tapered, basal half practically straight, remainder first curving fairly strongly inwards and then feebly outwards. Endomeral complex more or less pyriform, the endomeres terminating at about two-thirds length of parameres in strongly hooked outwardly-directed points. Penis stout, strongly curved (in dissections), extending far beyond tips of endomeres.

Female (Pl. I, fig. 10).—Length 1·82–1·97 mm. First tergite medially divided or deeply incised, second and third deeply incised, fourth incised to beyond middle, fifth to middle, sixth and seventh slightly incised. Abdomen 2·9–3·1 times as long as broad.

Type-material.—The only surviving syntype is a female in the Denny collection in the British Museum (Natural History). This is in poor condition, but we can see no characters that show it not to be the species redescribed above.

Other material examined.—45 males and 52 females from *Tringa ochropus* Linn., British Isles, Uganda, Tanganyka Territory and Afghanistan.

Quadraceps waterstoni sp. n.

(Fig. 9; Pl. II, figs. 11, 12.)

Type host: *Tringa solitaria* Wilson.

A moderately narrow, very dark, species. Lateral outlines of clypeus straight.

Male (Pl. II, fig. 11).—Length 1·40 mm. First abdominal tergite completely divided, that of second segment incised to well beyond middle, that of third nearly or quite to middle, those of fourth to sixth segments slightly incised, tergites of seventh and eighth segments divided. Abdomen 2·4–2·8 times as long as wide.

Genitalia (fig. 9) very reminiscent of those of *ochropi*, but parameres shorter, broader and more strongly curved, and endomeral complex with much more convex sides. Basal plate short, broadest at base and the lateral bars exceptionally broad basally.

Female (Pl. II, fig. 12).—Length 1·68–1·85 mm. First abdominal tergite divided, second and third deeply incised, fourth and fifth divided to middle, fifth and sixth slightly incised. Abdomen 2·8–2·9 times as long as broad.

Holotype male and *allotype* female from *Tringa solitaria* Wilson, COLOMBIA: Bolivar, 5.ix.1913.

Other material examined.—Two male and 3 female paratypes from *Tringa solitaria*, Colombia, Paraguay and Massachusetts.

Quadraceps conformis (Blagoveshtchensky), 1940.

(Fig. 10; Pl. II, figs. 13, 14.)

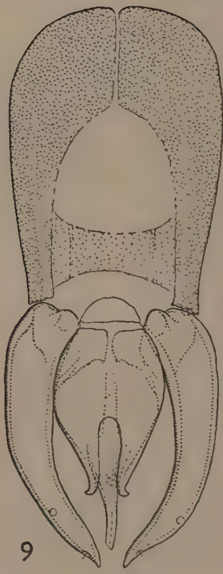
Type host: *Tringa totanus totanus* (Linn.).

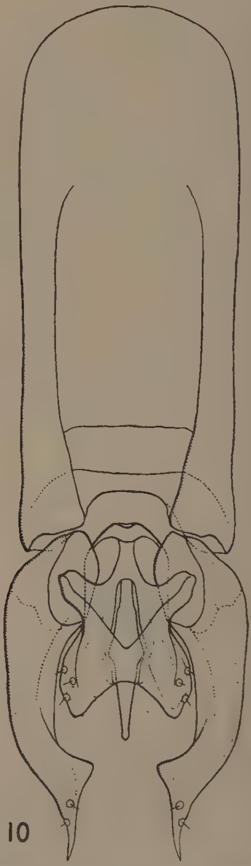
Degeeriella "*furva* Nitzsch"; Fresca, 1925 (*nec* Burmeister, 1838), *Eos, Madr.* **1**: 286, fig. 7 (male genitalia).

Degeeriella conformis; Blagoveshtchensky, 1940, *Mag. Parasit., Leningr. & Moscow*, **8**: 56, 84, fig. 14.

Degeeriella conformis Blagoveshtchensky; Blagoveshtchensky, 1948, *Mag. Parasit., Leningr. & Moscow*, **10**: 285, fig. 19 (male genitalia).

Quadraceps conformis (Blagoveshtchensky); Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga*: 310.





Figs. 9–10.—(9) *Q. waterstoni* sp. n. Genitalia of male paratype, from *Tringa solitaria*, Riacho, Paraguay. (10) *Q. conformis* (Blagoveschtchensky). Genitalia of male from *Tringa totanus*, Shetland Isles.

Originally described, from the female only, from material collected from *Totanus totanus totanus* (now *Tringa totanus totanus*), from Kumbashi, Talysh Lowlands, Azerbaijan. Blagoveshtchensky's later description of the male is from material from the same host-species.

A rather pale brown, moderately stout, species with lateral margins of the clypeus straight.

Male (Pl. II, fig. 13).—Length 1·40–1·50 mm. Tergal plate of first segment divided, those of second and third segments deeply incised, that of the fourth incised to half, that of the fifth slightly notched, those of the sixth to eighth segments divided. Sixth segment without tergocentral setae. Abdomen 1·8–1·9 times as long as wide.

Genitalia (fig. 10).—Basal plate moderately long, straight-sided, with a sclerotic transverse bar near its distal end. Parameres unlike those of any other species, rather short, their inner side extended into a triangular lobe beyond which the paramere bends outwards and tapers to a sharp point. Endomeres forming two short wing-like lobes between which the fairly long spindle-shaped penis projects.

Female (Pl. II, fig. 14).—Length 1·65–1·82 mm. Tergite of first segment of abdomen divided, those of the second to fifth segments deeply, that of the sixth feebly, and that of the seventh hardly at all incised. Abdomen 2·3–2·5 times as long as wide.

Material examined.—150 males and 123 females from *Tringa totanus totanus* (Linn.), *T. totanus britannica* Mathews,[5] *T. totanus robusta* (Schiøler) and *T. totanus terrignotae* Meinertzhagen and Meinertzhagen,[5] British Isles, Finland, Czechoslovakia, Morocco, Sudan, Nepal and India.

Quadraceps ravus (Kellogg), 1899.

(Fig. 11 ; Pl. II, figs. 15, 16.)

Type host : *Actitis macularia* (Linn.).

Nirmus furvus var. *ravus* Kellogg, 1899, *Occ. Pap. Calif. Acad. Sci.* **6** : 14, pl. 2, fig. 1.

Degeeriella rava Kellogg ; Harrison, 1916, *Parasitology*, **9** : 122.

Degeeriella subfusca Blagoveshtchensky, 1948, *Mag. Parasit. Leningr. & Moscow*, **10** : 286, figs. 20, 20*a*.

Quadraceps ravus (Kellogg) ; Hopkins and Clay, 1952, *Check List of the Genera and Species of Mallophaga* : 316.

Quadraceps subfuscus (Blagoveshtchensky) ; Hopkins and Clay, 1952, *l.c.* : 317.

Kellogg's original description was of a female from *Actitis macularia* from Panama. Blagoveshtchensky had six males and fifteen females from *Actitis hypoleucus*.

A moderately stout dark brown species. Margins of clypeus not straight but compressed in a concave manner and thus becoming reminiscent of the shape of head in *Saemundssonia*.

Male (Pl. II, fig. 15).—Length 1·27–1·34 mm. Tergal plate of first segment divided, that of the second deeply and those of the third to fifth more shallowly incised, those of sixth to eighth segments divided in the middle line. Abdomen 1·6–1·8 times as long as wide.

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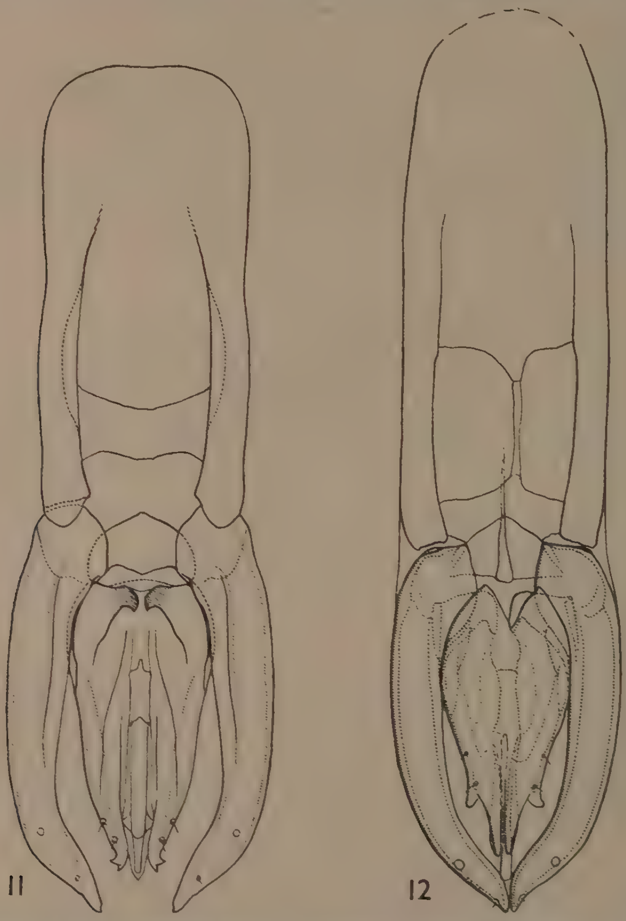
[5] Peters calls the British subspecies *T. totanus bewickii* (Rennie), but according to Witherby, Jourdain, Ticehurst and Tucker (1948, *Handbook of British Birds*, **4** : 324) Rennie's name does not refer to the redshank but to the ruff. Peters places *T. totanus terrignotae* as a synonym of *T. t. eurhinus* (Oberholzer) but notes an unresolved controversy about this synonymy.

Genitalia (fig. 11): Basal plate with a sclerotic transverse bar joining the two lateral bars. Parameres slender, nearly straight to about three-quarters where they bend slightly inwards. Endomeres closely bound together with penis and other structures to form an elongate, roughly pyriform, complex extending nearly to the tips of the parameres, tips of endomeres bidentate and extending to almost the same point as the apex of the penis.

Female (Pl. II, fig. 16).—Length 1·49–1·63 mm. Tergal plate of first segment divided, those of second and third segments deeply incised and that of the fourth incised to a half. Abdomen 1·9–2·2 times as long as wide.

We are unable to distinguish specimens from *Actitis macularia* from those from *Actitis hypoleucos*.

Material examined.—Redescribed from 8 males and 7 females from *Actitis macularia* (Linn.) from U.S.A. and Costa Rica. We have also examined



Figs. 11–12.—(11) *Q. rarus* (Kellogg). Genitalia of male from *Actitis hypoleucos*, Fochabers, Moray, Scotland. (12) *Q. impar* sp. n. Genitalia of male holotype.

39 males and 48 females from *Actitis hypoleucos* (Linn.), from British Isles, Liberia, Sudan, Uganda, Nepal and Philippine Isles.

Quadraceps impar sp. n.

(Fig. 12, ; Pl. II, figs. 17, 18.)

Type host : *Heteroscelus brevipes* (Vieillot).

This species is noteworthy for its marked sexual dimorphism, the male being relatively very much smaller and broader-headed than the female (cephalic index of male 0·85, of female 0·71). The lateral margins of the clypeus are straight.

Male (Pl. II, fig. 17).—Length 1·35 mm. In the sole specimen available the divisions of the tergites cannot be distinguished satisfactorily. Abdomen 1·7 times as long as broad.

Genitalia (fig. 12) : Basal plate parallel-sided, the lateral sclerotic rods joined by a weakly sclerotised transverse bar. Parameres rather slender, uniformly and rather weakly curved to just before the tips, which are curved outwards. Endomeral complex elongate oval, the endomere of each side terminating in a blunt projection at the level of about five-eighths of the length of the parameres. Penis straight, extending nearly to apex of parameres, surrounded by telomere to shortly before its apex but the latter free.

Female (Pl. II, fig. 18).—Length 1·62–1·81 mm. First tergite divided, second to fifth deeply notched and sixth incised nearly to middle ; at apex of each incision a markedly darker patch of pigment. Abdomen 1·8–1·9 times as long as broad.

Holotype male and *allotype* female from *Heteroscelus brevipes* (Vieillot), Saghalin, Meinertzhagen collection, slide no. 11013*a*.

Other material examined.—Two female paratypes from *Heteroscelus brevipes* (Vieillot), Saghalin, and one female from *Heteroscelus incanus* (Gmelin) from California. *H. brevipes* is regarded by some ornithologists as a subspecies of *H. incanus*, but Peters treats them as specifically distinct.

Quadraceps carrikeri sp. n.

(Fig. 13 ; Pl. II, figs. 19, 20.)

Type host : *Catoptrophorus semipalmatus inornatus* (Brewster).

As in the preceding species, the difference in size between the sexes is somewhat considerable. Lateral margins of clypeus straight.

Male (Pl. II, fig. 19).—Length 1·52–1·67 mm. First abdominal tergite apparently divided, second and third tergites incised to beyond middle, fourth to sixth only slightly notched, seventh and eighth divided. Abdomen 2·1 times as long as broad.

Genitalia (fig. 13).—Basal plate with margins markedly sinuate, convex basally and distally but concave in the middle, with a transverse sclerotic bar joining the two lateral rods. Parameres short, exceptionally broad and strongly curved. Endomeral complex regularly oval, the endomeres without lateral projection. Penis short and straight, extending little beyond apex of endomeral complex.

Female (Pl. II, fig. 20).—Length 1·91–2·06 mm. First tergite probably completely divided, second to fifth deeply incised, sixth either incised to middle or only slightly notched. Abdomen 2·6 times as long as broad.

Holotype male and *allotype* female from *Catoptrophorus semipalmatus inornatus* (Brewster), CALIFORNIA: San Diego, March 1939, Meinertzhagen collection, slide no. 12898.

Other material examined.—21 male and 18 female paratypes from *C. semipalmatus inornatus*, from California and Texas.

Q. impar and *Q. carrikeri* show no indications of particularly close relationships either with the other species or with one another; the latter species, in particular, stands wholly apart.

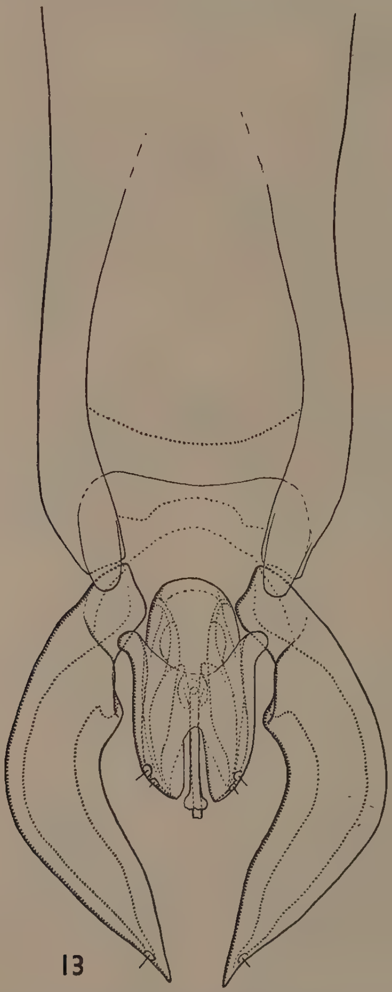


FIG. 13.—*Q. carrikeri* sp. n. Genitalia of male paratype from *Catoptrophorus semipalmatus inornatus*, San Diego, California.

Species incertae sedis.

Quadraceps naumanni (Giebel), 1874.

Nirmus naumanni; Giebel, 1874, *Insecta epizoa* : 163.
Quadraceps naumanni (Giebel); Hopkins and Clay, 1952, *Check List of Genera and Species of Mallophaga* : 313.

The host of this species is given as "*Totanus gilvipes*," which is apparently not the name of any bird. The description is utterly inadequate, and there seems to be no possibility of identifying the species now that the syntypes are lost. It has been suggested to us that the host-name may have been a slip for *T. flavipes*, but the description does not fit the *Quadraceps* found on the latter and the name *naumanni* must be regarded as inapplicable.

Quadraceps major (Kellogg).

Nirmus fissus var. *major*; Kellogg, 1899, *Occ. Pap. Calif. Acad. Sci.* **6** : 15, pl. 2, fig. 2.
Quadraceps major (Kellogg); Hopkins and Clay, 1952, *Check List of . . . Mallophaga* : 313.

We have not been able to identify this species owing to the inadequacy and probable incorrectness of the host-record. The species was described from "Several specimens, including male, female and immature specimens, from *Tringa* sp. (Baja California)." The facies of the insect is, however, that of the group of *Quadraceps* found on the Charadriinae, and we think the host-record is almost certainly incorrect. Professor Ferris has kindly searched in the Kellogg collection for the syntypes but is unable to find them.

AVIPARASITOLOGICAL CONTRIBUTIONS TO THE SYSTEMATICS OF THE TRINGINAE.

Some ornithologists use the genus *Tringa* in a very wide sense, while others split it up into a number of genera. Peters rejects many of the subdivisions but recognises *Pseudototanus*, *Xenus*, *Actitis*, *Catoptrophorus* and *Heteroscelus*. From an aviparasitological point of view there is no objection to the inclusion of all the species in one genus, *Tringa*, but in that case *Actitis*, *Catoptrophorus* and *Heteroscelus* ought also to be suppressed because, parasitologically speaking, there are no characters which would justify our placing the species referred to these groups apart from all the others. We cannot decide how far this applies also to the genera *Pseudototanus* and *Xenus* because we have not been able to examine any *Quadraceps*-material from birds of these two genera, but the presence on *Xenus* of a species of the genus *Carduiceps*, whose occurrence on a given host seems to be at least usually incompatible with the occurrence of *Quadraceps*, suggests the probability that *Xenus* is more distinct than the other groups concerned.

The alternative to placing all the birds closely related to *Tringa* in one large single group, as was done by Hartert, is to attempt to split them into numerous smaller groups, as was done by Lowe (1931), on the basis of anatomical investigations and (following him) by Peters (1934). Aviparasitology supports the view that this second solution accords better with natural relationships than the first, although on the basis of parasitology we would make use of a somewhat different grouping from that of Lowe. The latter refers three species (*ochropus*, *solitaria* and *glareola*) to the genus *Tringa*, but states at the same time that he is strongly inclined to separate *T. glareola* from the other two species and place it in a separate genus, *Rhyacophilus*. This suggestion is entirely supported by aviparasitology, for the *Quadraceps*-species from *Tringa ochropus* and *T. solitaria* have male genitalia of the same type and undoubtedly belong together, whereas the species parasitic on *T. glareola* belongs to a quite different type. Hartert was unquestionably right when he emphasised that *T. solitaria* reminded him very forcibly of *T. ochropus*, a suggestion also accepted by Lowe (1931 : 723) and by Witherby *et al.* (1948).

Tringa stagnatilis shows aviparasitologically an extremely close relationship with *T. glareola* and a somewhat more remote one with the North American *T. flavipes*. *Tringa totanus*, *T. erythropus*, *Catoptrophorus semipalmatus* and *Heteroscelus brevipes* all stand quite alone (except that entirely inadequate evidence places *H. brevipes* with *H. incanus*), while on the other hand *T. melanoleuca* and *T. nebularia* seem to constitute a natural group. Here, also, Hartert seems to show the soundness of his feeling for phylogenetic relationships when he remarks that, judging by its size and general appearance, *T. melanoleuca* must be very close to *T. nebularia*. On the other hand, parasitology does not suggest any justification for the recognition as natural entities of the genera *Totanus* and *Glottis* (both *sensu* Lowe, the former comprising the species *totanus*, *flavipes*, *melanoleuca* and *erythropus*, the latter *nebularia*, *stagnatilis* and *guttifer*). The linking together of *Actitis macularia* and *A. hypoleucos* is entirely supported by the evidence derived from their parasites.

Summary.

The species of the genus *Quadraceps* occurring on Tringinae have been much confused but are easily separable by means of differences in the male genitalia. The known species are redescribed in this paper and three new species are described; in all instances photographs of both sexes and line-drawings of the male genitalia are given. The possible bearing of the distribution of these Mallophaga on the relationships of their hosts is briefly discussed.

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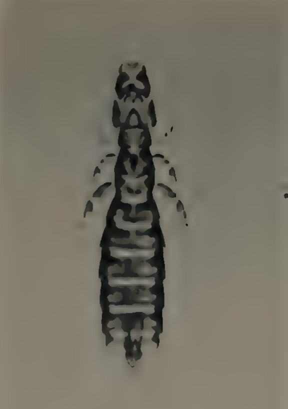
PLATE I.

Fig. 1.—*Quadraceps obscurus* (Burmeister). Male neotype.
Fig. 2.—The same. Female neallotype.
Fig. 3.—*Q. falcigerus* (Peters). Male, from *Tringa flavipes*, California.
Fig. 4.—The same. Female, from *Tringa flavipes*, California.
Fig. 5.—*Q. similis* (Giebel). Male neotype.
Fig. 6.—The same. Female neallotype.
Fig. 7.—*Q. furvus* (Burmeister). Male neotype.
Fig. 8.—The same. Female neallotype.
Fig. 9.—*Q. ochropi* (Denny). Male, from *Tringa ochropus*, Namanve, near Kampala Uganda.
Fig. 10.—The same. Female, data as for male.

PLATE I.



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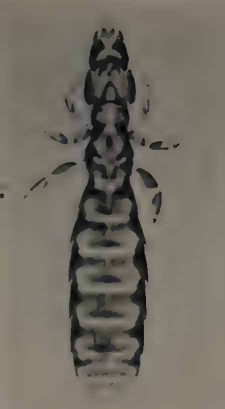

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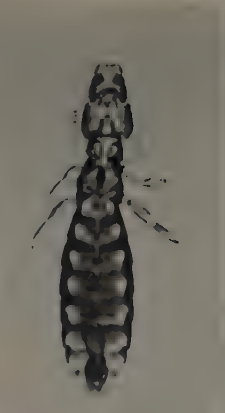

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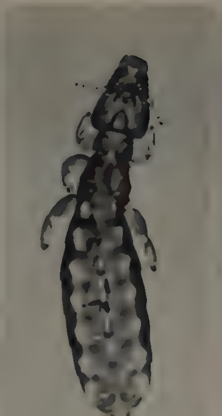

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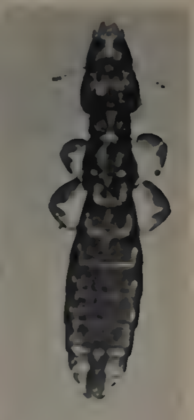

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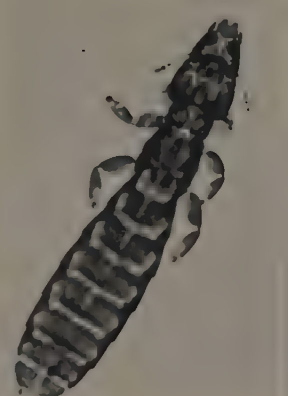

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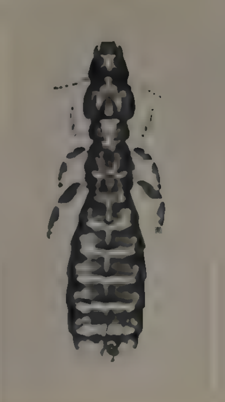

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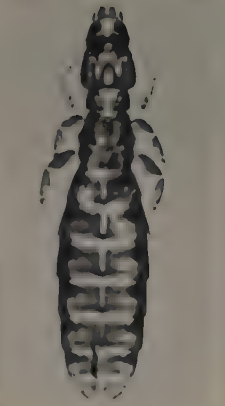

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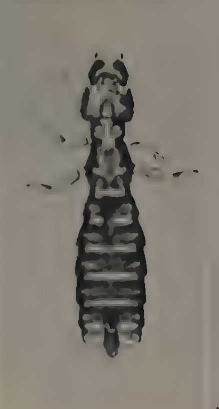

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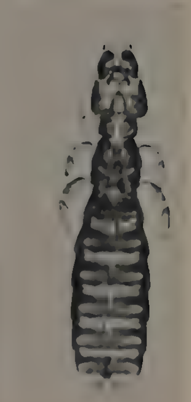

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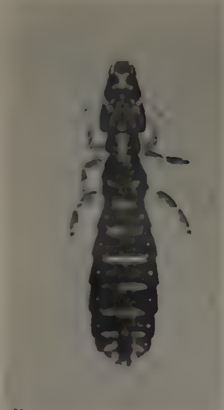
PLATE II.

Fig. 11.—*Quadraceps waterstoni* sp. n. Male holotype.
Fig. 12.—The same. Female allotype.
Fig. 13.—*Q. conformis* (Blagovestchensky). Male, from *Tringa totanus britanniae*, Orkney Isles.
Fig. 14.—The same. Female, data as for male.
Fig. 15.—*Q. ravus* (Kellogg). Male, from *Actitis macularia*, Costa Rica.
Fig. 16.—The same. Female, data as for male.
Fig. 17.—*Q. impar* sp. n. Male holotype.
Fig. 18.—The same. Female allotype.
Fig. 19.—*Q. carrikeri* sp. n. Male holotype.
Fig. 20.—The same. Female allotype.

PLATE II.



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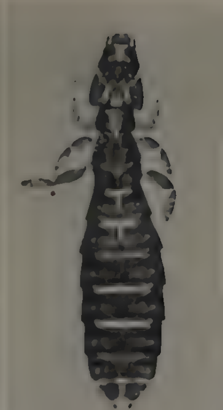

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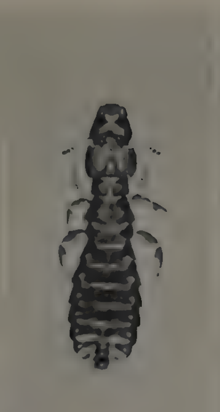

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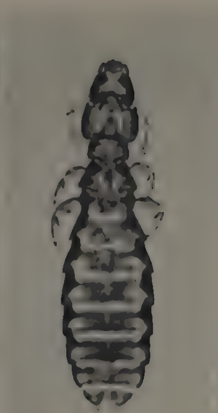

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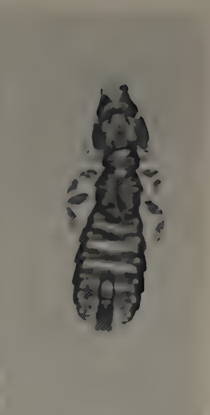

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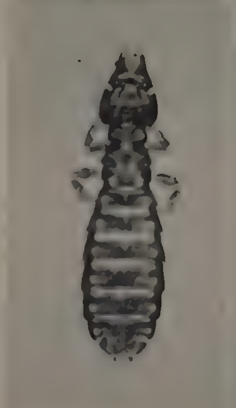

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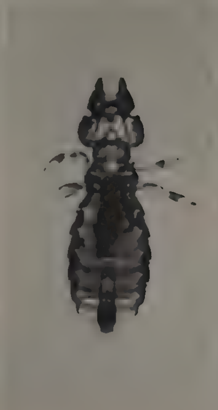

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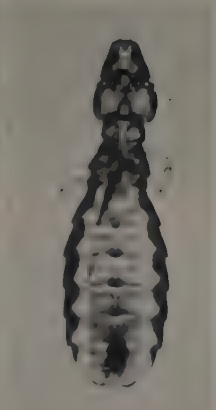

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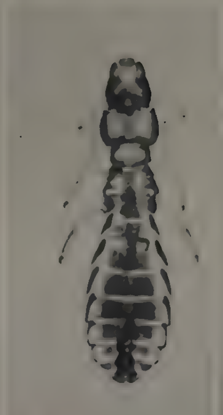

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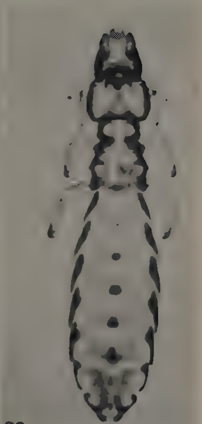

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Vol. 105. Part 9. Pp. 151–162. 15 figs. 30th June, 1954

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CLASSIFICATION OF THE XIPHYDRIIDAE (HYMENOPTERA).

By Robert B. Benson, M.A., F.R.E.S.

Manuscript received 22nd October, 1953.

(Read 4th November, 1953.)

With 15 Text-figures.

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1. Introduction.

Ashmead (1898) and Rohwer (1911) divided the Xiphydriidae into two subfamilies (Xiphydriinae and Derecyrtinae) based on the form of the pronotum and the presence or absence of vein rm^2 in the fore wing. Maa (1949) has recently proposed an entirely new classification, with 5 subfamilies, based mainly on the number of segments in the maxillary and labial palps. Maa's paper is a most valuable contribution to the study of these insects and he has collected together much new morphological detail from his rich collections in Asia, especially by his investigations of the mouthparts. But I cannot at all accept his conclusions on the classification of the family; and this paper has been written to put forward a new system based on entirely different criteria.

2. Available Material.

The first difficulty in studying the Xiphydriidae (and the same applies to several other archaic sawfly families) is the lack of material in collections. Many of the described species are known only from one or two specimens, so that it is almost certain that many more species await discovery. The family is known from all the temperate and tropical forest regions of the world, including New Zealand, except that it has not yet been found in Africa or Madagascar. The host-plant associations are unknown except for a few holarctic species whose larvae bore in the wood of certain angiosperm trees.

Apart from the British species *Xiphydria camelus* L. and *prolongata*

Geoffroy, I have before me now only 57 specimens belonging to 32 species (2 undescribed) out of 84 now known from the world, but the material before me includes, through the kindness of Professor G. C. Varley, the types of Westwood and Smith from the Hope Department, Oxford.

Maa in his study adds 11 new genera and subgenera to the 8 previously recognised, and 6 of these 11 are monotypic, so that nearly half of the genera and subgenera described up till now are monotypic (9 out of 19); and 8 of the new species he describes are based on single specimens. His new genera *Indoxiphia* (with its subgenus *Cingalixiphia*) and *Eoxiphia* as well as his interpretation of the South American genera *Derecyrta* and *Brachyxiphus* are not based on any specimens he has ever seen, but are deduced entirely from earlier descriptions.

3. The Significance of Characters in Showing Relationship.

Maa's system of classification is not convincing because he has not shown that the number of segments in the labial and maxillary palps correlate well with other characters. A study of natural classification is primarily a study of character correlations. A major group, such as a subfamily, is simply a group of genera sharing through descent a certain set of correlated characters, and only by studying the correlations can we deduce the natural relationships with any confidence.

It is not enough that he should point to the analogy with the Siricidae (Benson, 1943) or the Cephidae (Benson, 1946), where the forms of these palps have been found to correlate well with diverse other characters. The stability of an individual character, as is well known, may be quite different in related groups, fixed by linkage with other characters in one group, free and variable in another. Likewise the oldest group in a family is simply that group that has retained its character-correlations for the longest time. The mere presence of the same primitive character in different groups does not necessarily indicate close affinity, unless the character in each of the groups is bound in correlation with the same set of other characters. With specialised characters we have to consider whether parallel evolution and adaption to similar conditions are masking the true affinity.

4. The Tarsal Pulvilli.

I cannot find any previous mention of the bilobed tarsal pulvilli which seem to be characteristic of most Xiphydriidae and to distinguish them from all other sawfly families (and I believe hymenopterous families); they are conspicuous in *Brachyxiphus* and *Xiphydria* (fig. 7) but tend to obsolescence in the genera related to *Indoxiphia*; only in *Derecyrta* (*sensu restricta*) are they entirely absent and here instead the undersides of the tarsi are furnished with tufts of stout bristles (fig. 5).

The tarsal pulvilli thus show interesting differences in the different sawfly families (cf. Benson, 1945 : 28): in the Pamphiliidae, certain Xyelidae, and Siricidae the projecting flaps are missing, but the tarsal segments are excised apically beneath to expose a membranous area. In Orussidae they appear to be totally absent and the tarsi here resemble those of *Derecyrta* (*sens. restrict.*) in being furnished with tufts of stout bristles instead. In all other sawfly families simple pulvillar pads project from the apices of the tarsal segments.

5. The Subfamilies.

In the scheme I am proposing there are to be two subfamilies, the Derecyrtinae and the Xiphydriinae, though these are quite different from the two subfamilies of the same names proposed by Ashmead and adopted by Rohwer. Ashmead and Rohwer, for example, place *Brachyxiphus* with the Xiphydriinae, while I place it with the Derecyrtinae on all counts. Maa distinguishes a subfamily Derecyrtinae for *Derecyrta* (Neotropical), and a Brachyxiphinae for *Brachyxiphus* and *Eoxiphia* (both Neotropical) and also for a new genus *Nasoxiphia* (from E. Asia). Such a scheme to my mind does violence to the natural relationships because, as I shall show below, there are at least four correlated major characters, which link together *Derecyrta* and *Brachyxiphus* and distinguish them from *Nasoxiphia* (and also I believe *Eoxiphia*) and all the other genera of the Xiphydriidae. I cannot believe that this is not significant. Admittedly three of these characters have never been mentioned before and the fourth has been wrongly described, so that Maa, not having access to any actual *Derecyrtinae*, has been misled by earlier writers. These characters are as follows :

(a) *The Pronotum.*

Maa quotes Rohwer in saying that in *Derecyrta* the pronotum is not so deeply emarginate medially as in *Brachyxiphus* and in all other genera, and that in *Derecyrta* alone is there a distinct dorsal surface to the pronotum laterally. Actually the form of the pronotum in *Derecyrta*, *Steirocephala* gen. n. and in *Brachyxiphus* is almost identical, but sharply distinguished from that of all the other Xiphydriidae. In *Derecyrta*, *Steirocephala* gen. n. and *Brachyxiphus*, when the pronotum is looked at from above, the emargination in front is scarcely longer than the medial length of the remaining portion, while in all other Xiphydriidae the emargination here is several times greater than the medial length of the remaining portion of the pronotum which is scarcely as long as a single tegula (cf. figs. 10 and 11 with fig. 12).

(b) *The Femora.*

The slim femora of *Derecyrta*, *Steirocephala* gen. n. and *Brachyxiphus*, especially in the hind legs (figs. 1 and 2), are in contrast to the swollen femora of all the other Xiphydriidae I have examined (see figs. 3 and 4).

(c) *The Hind Tarsal Claws in the Female.*

In all *Derecyrta*, *Steirocephala* gen. n. and *Brachyxiphus* the hind tarsal claw and claw-bearing segment are noticeably enlarged in the females (figs. 1 and 2)—the hind claw being at least one-and-a-half times as long as the middle claw. In all other Xiphydriidae the hind claw is scarcely longer than the middle claw (figs. 3 and 4).

(d) *Mesoscutellum.*

In all *Derecyrta* (*s.l.*) and *Brachyxiphus*, but in no other Xiphydriidae, there is a clearly defined area surrounded by a carina and covering the front and middle parts of the mesoscutellum and containing a large solitary tubercle near its apex.

These four characters link *Derecyrta*, *Steirocephala* gen. n. and *Brachyxiphus* (all restricted to South America) and distinguish them at once from all other Xiphydriidae. The form of the pronotum and the femora might be regarded as primitive characters and the enlarged hind tarsal claws as adaptive, perhaps serving some purpose in oviposition; but as they occur correlated with a special ornamentation of the scutellum there is no escaping the conclusion that they signify a closer relationship of these three genera than either is to any other Xiphydriid. The absence of the vein 2*r* in the fore wing of *Derecyrta* and *Steirocephala* gen. n. (and in a new genus *Xiphidiaphora* of Xiphydriinae I am describing below but not in *Brachyxiphus*), the absence of the tarsal pulvilli only in *Derecyrta* (but not in *Brachyxiphus* or in a new Derecyrtine genus *Steirocephala* I am describing below), and the primitive form of head in *Brachyxiphus* alone, are all treated here as secondary characters because they are not correlated as are the four characters mentioned above.

Maa segregates the Derecyrtinae from the Brachyxiphinae, and splits the rest of the Xiphydriinae into three more subfamilies; thus by inference he attributes equal status to each of the five groups. I find this totally unacceptable, especially as he links *Eoxiphia* (from S. America) and *Nasoxiphia* (from E. Asia) with *Brachyxiphus* into his Brachyxiphinae solely because they are all supposed to have the same number of segments in their labial and maxillary palps (4 and 6), a combination not known to occur in any other Xiphydriid genera; actually the *Brachyxiphus* specimens I have examined all have 4 and 7 segments respectively.

6. THE TRIBES OF DERECYRTINAE.

The three genera ascribed to Derecyrtinae, *Brachyxiphus*, *Derecyrta* and *Steirocephala* gen. n. are very distinct from each other: but on the whole *Brachyxiphus* is more distinct than the other two and I am proposing two tribes: the Derecyrtini for *Derecyrta* and *Steirocephala* gen. n.; and the Brachyxiphini for *Brachyxiphus*, characterised by the retention of vein 2*r* in the fore wing and the possession of a dull, heavily sculptured, densely pilose head unlike that of any other known Xiphydriid, though showing its nearest approach in the new Xiphydriine genus *Gryponeura* which is described below.

7. THE TRIBES OF XIPHYDRIINAE.

It is a very different problem trying to segregate into tribes the 20 genera of the Xiphydriinae. And though some of these may be fused together into larger genera with the increase of knowledge, further new genera are almost certain to be discovered. Unfortunately I have not seen any representative of almost half of the previously described genera (8 out of 17); and, as some of the characters that might be used have not been used in the same way before and cannot be recovered with certainty from earlier descriptions, I have enclosed below in brackets all genera of which I have seen no adequate representative. It is necessary first to discuss some of Maa's segregates based on the number of segments in labial and maxillary palps and on the form of the pre-episternum; then some other characters and possible segregates will be considered.

(a) *Labial and Maxillary Palps.*

In Maa's system the Hyperxiphiinae are characterised by having 4-segmented labial palps and the Xiphydriinae by having them 3-segmented. Maa places *Indoxiphia* in his Xiphydriinae; but, though the type of the species which Maa calls *Indoxiphia* (*Cingalixiphia*) *striatifrons* (Cameron) has a 3-segmented labial palp, the type of *Indoxiphia* (*I.*) *indonesica* Forsius has it 4-segmented. In *Xiphydria longicollis* Geoffroy (3 ♀ examined), *X. picta* Konow (2♂, 1♀) *X. popovi* Sem. & Guss. (1 ♀) and *X. scutellata* Sem. & Guss. (1 ♂, 1 ♀) the labial palp is 4- and not 3-segmented; and in some *X. prolongata* Geoffroy and *X. camelus* L., the apical segment of the labial palp is more or less divided into two segments and the maxillary palp can be 4- or 5-segmented (as in figs. 1 and 2). Therefore, if these genera are to remain intact and remain in the Xiphydriinae, the group must be redefined as having labial palps 3- to 4-segmented and maxillary palps 4- to 5-segmented, thus breaking down his major division between his Xiphydriinae and his Hyperxiphiinae. And, as both *X. prolongata* and *X. camelus* (the type if *Xiphydria*) have a sensory pit in the swollen apical segment of the labial palp, it is impossible to maintain his further subfamily Euxiphydriinae characterised mainly on this basis. On the other hand *Moaxiphia* (New Zealand) and a new related genus *Rhysacephala* (Australia), which I am describing below, have their 7-segmented maxillary palps longer than the 4-segmented labial palps, unlike all the other Xiphydriinae I have examined. These might then form a tribe together with *Eoxiphia* and possibly a few other genera which, though they have 6 or even fewer segments in the maxillary palps, yet have these palps longer than the labial ones.

(b) *Pre-episternum.*

I have failed to appreciate Maa's description of "the pre-episterna" as being "in profile slightly longer than high" by which, together with slight venational differences, he segregates his tribe Konowiini of Xiphydriinae from Xiphydriini of Xiphydriinae, as well as from Euphydriinae and Hyperxiphiinae, which he says have the "pre-episterna . . . in profile distinctly much longer than high."

(c) *Malar Space.*

It is not clear how Maa has measured the shortest length of the malar space which he gives in his descriptions. When the adults are at rest each antenna tends to lie forward between the eye and the base of the mandible across the malar space, and there is a groove more or less developed here in which the antenna rests, as Maa has himself remarked: I shall call this the "antennal groove" (fig. 13). In some genera the groove is well developed with a carinate orbital margin parallel to the eye margin and very close to it, but whether this groove is defined or not there is always a very deep rounded depression, often with a carinate margin, extending from the middle of the malar edge adjoining the mandible base (I am calling this the "malar depression"); and depression and groove are often confluent (figs. 13 and 14).

When Maa describes the malar space as very short I take it to mean that the antennal groove is clearly defined and reaches close to the eye margin (fig. 13), as this agrees with his descriptions of genera I have examined and is typical of Australian, most Oriental and some of the Eastern Palaearctic genera of Xiphydriinae (i.e., *Cingalixiphia*, (*Genaxiphia*), *Gryponeura* gen. n., *Indoxiphia*, *Moaxiphia*, *Palpixiphia*, (*Platyxiphydria*), *Rhysacephala* gen. n. (*Xiphydriola*) and *Xiphidiaphora* gen. n.); and in these genera also the orbital edge of the antennal groove coincides with the inner edge of the malar depression.

In the Palaearctic genera *Euxiphydria*, *Konowia s.l.* (*Nasoxiphia*), and most *Xiphydria*[1] as well as in the oriental genera (*Dryxiphia*), *Hyperxiphia* and (*Paraxiphia*) the malar depression is set far from the eye margin and the antennal groove is not clearly defined,[2] or, if it is defined by a carinate orbital margin, this does not coincide with the inner margin of the malar depression (fig. 14).

(d) *Wing Venation.*

Konowia s.l. has the anal cell of the fore wing constricted near the base and cell $3R_1$ in the fore wing and R_1 in the hind wing open apically; but these very tendencies are also shown in the closely related genus *Xiphydria*: there is, for example, considerable variation between the different species as to the amount that the anal cell of the fore wing is contracted towards the base; and in certain species (e.g., *X. prolongata* Geoffroy) cell $3R_1$ in the fore wing is actually open at the apex; and in other species (e.g., *X. maculata* Say) cell R_1 of the hind wing is open apically as well.

On the other hand, in the genera *Indoxiphia*, *Moaxiphia* and *Rhysacephala* gen. n. there is an entirely different tendency; the apical portion of the anal cell is open through the more or less fading out of the vein A_2 just before the cross-vein.

(e) *Sawsheath-basal Plate Ratio.*

In *Euxiphydria* (*Genaxiphia*), *Gryponeura* gen. n., *Hyperxiphia*, *Konowia s.l.*, (*Nasoxiphia*), (*Paraxiphia*), and *Xiphydria* the sawsheath is about as long as the basal plate.

On the other hand, in *Cingalixiphia*, (*Dryxiphia*), *Indoxiphia*, *Moaxiphia*, *Palpixiphia*, (*Platyxiphydria*), *Rhysacephala* gen. n., *Xiphydiaphora* gen. n., and (*Xiphydriola*) the sawsheath is shorter than the basal plate, the ratio of sawsheath to basal plate being 1·0 : 1·2 to 1·5.

8. SUMMARY OF CLASSIFICATION.

1. Pronotal collar less excavated in front (so that its total excavation is at most scarcely longer than the medial length remaining, which itself is several times the length of a tegula) (figs. 10 and 11). Mesoscutellum with a dorsal area margined by a carina and including a prominent tubercle near its apex. Femora scarcely swollen (hind femur with its trochantellus four to seven times as long as broad) (figs. 1 and 2). Hind claw-bearing tarsal segment much enlarged in female and hind claw at least one-and-a-half times as long as middle claw. Sawsheath of female only about half to five-eights as long as basal plate. Labial palp 3- to 4-segmented; and maxillary palp 6- to 7-segmented. Restricted to S. America. (**Derecyrtinae**) . . . . 2.

[= Derecyrtinae as part of Brachyxiphinae of Maa.]

---

[1] With the exception of *X. prolongata* Geoffroy, *X. buyssoni* Konow and possibly others.

[2] In the neotropical Derecyrtinae also no clearly defined antennal groove is visible across the genae.

Pronotal collar deeply excavated in front (so that the total excavation is several times deeper than the remaining medial length which itself is less than the length of a tegula) (fig. 12). Mesoscutellum without any dorsal area defined by a carina and there is no prominent tubercle near its apex, though the whole may be coarsely sculptured. Femora more swollen (hind femur with its trochantellus only about three to three-and-a-half times as long as broad) (figs. 3 and 4). Hind claw-bearing tarsal segment in female not abnormally enlarged and hind claw not one-and-a-half times as long as the middle claw. Sawsheath of female from five-eighths to as long as the basal plate. Labial palp 3- to 4-segmented and maxillary palp 4- to 7-segmented. [Tarsi with pulvilli.]

Cingalixiphia Maa, *Dryxiphia* Maa, ? *Eoxiphia* Maa, *Euxiphydria* Sem. & Guss., *Genaxiphia* Maa, *Gryponeura* gen. n., *Hyperxiphia* Maa, *Indoxiphia* Maa, *Konowia* Brauns (= *Apoxiphia* Maa and *Pseudoxiphydria* Enslin), *Moaxiphia* Maa, ? *Nasoxiphia* Maa, *Palpixiphia* Maa, *Paraxiphia* Maa, *Platyxiphydria* Takeuchi, *Rhysacephala* gen. n., *Xiphidiaphora* gen. n., *Xiphydriola* Sem. & Guss., and *Xiphydria* Latreille **Xiphydriinae, Xiphydriini.**

[= part of Brachyxiphinae, Moaxiphinae, Hyperxiphinae, Euxiphydriinae and Xiphydriinae of Maa.]

2 (1). Fore wing with vein 2*r* absent. Head with temples almost impunctate behind and glabrous. Hind femur more swollen medially (so that it is only four to five times as long as broad). Hind apical tarsal segment of female shorter than basitarsus. Labial palp 3- to 4-segmented ; maxillary palp 6- to 7-segmented. Tarsi with or without pulvilli. *Derecyrta* Smith and *Steirocephala* gen. n. **Derecyrtini.**

Fore wing with vein 2*r* present. Head dull with dense sculpture and profuse pubescence. Hind femur very slender (at least seven times as long as broad). Hind apical tarsal segment of female enormously enlarged so that it is longer than the basitarsus. Labial palp 4-segmented ; maxillary palp 7-segmented. Tarsi with pulvilli. *Brachyxiphus* Phillipi . . . **Brachyxiphini.**

9. DESCRIPTIONS OF NEW GENERA AND SPECIES.

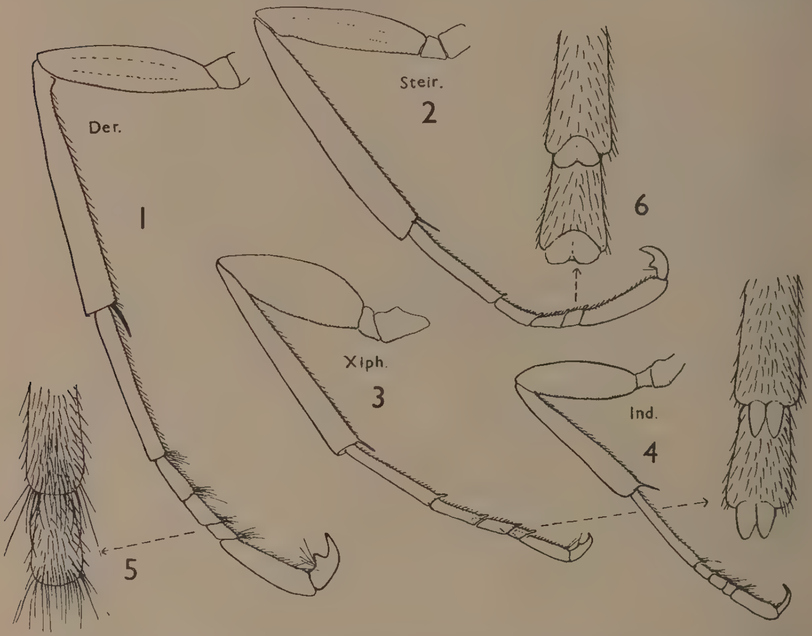
Steirocephala gen. n.

Belongs to the Derecyrtini of the Derecyrtinae as defined above.

Head about as wide as thorax, parallel-sided, impunctate behind ocelli and eyes ; in addition to the postgenal-postoccipital carina the genal carina is strongly developed up to the level of the middle of the eye ; mandible normal ; labial palp 4-segmented with the apical segment almost as long as the 1st and clavate ; maxillary palp 7-segmented and much longer than the labial palp and slender apically ; malar depression on gena with a raised carinate margin ; posterior ocelli in the supra-orbital line. *Antenna* setaceous, 18- to 24-segmented ; scape and pedicel elongate ; 3rd segment about as long as scape and longer than 4th and 5th together. *Thorax* and *wings* as in *Derecyrta*. Hind femur scarcely swollen medially (together with trochantellus 4–5 times as long as broad) ; tarsi normal with short bilobed pulvilli (fig. 6) and not clothed conspicuously with bristles on the underside ; hind claw of female about one-and-a-half times as long as middle claw. *Abdomen* about one-and-a-half times as long as head and thorax together, and definitely contracted basally; sawsheath about two-thirds as long as basal plate; ovipositor about as long as hind tarsus.

Type species: *Derecyrta reedii* W. F. Kirby, 1882. Distribution: CHILE. Contains also the species *D. flavipes* Phillippi and *D. ruficeps* Brullé.

The new genus is closely related to *Derecyrta* but distinguished by having the genal carina developed on the lower lateral margin of the head as well as the post-genal post-occipital carina and also by having distinct bilobed tarsal pulvilli on the legs, as in most Xiphydriidae except *Derecyrta* (where the pulvilli on the tarsi are obsolete and where the tarsi instead are clothed beneath with a dense mat of stiff bristles). In general appearance representatives of the new genus are stouter than *Derecyrta* and have the abdomen only about one-and-a-half times as long as head and thorax together (instead of twice as long) and clearly contracted basally (instead of almost cylindrical).



FIGS. 1–7.—(1–4) Hind legs of female of: 1, *Derecyrta*; 2, *Steirocephala*; 3, *Xiphydria*; 4. *Indoxiphia*. (5–7) 3rd and 4th hind tarsal segments from beneath in: 5, *Derecyrta*; 6, *Steirocephala*; 7, *Xiphydria*.

Rhysacephala gen. n.

Belongs to Xiphydriinae as defined above.

Head about as wide as thorax, narrowed behind the eyes where it is divided medially by a longitudinal furrow or row of punctures, and often transversely striate on the temples and genae as far as the base of the mandibles; one of these striae represents the genal carina below; postoccipital carina also well developed; malar space from eye margin to inner edge of malar depression very short (as in fig. 13). Labial palp 3- to 4-segmented; basal and apical segments equal and much longer than the intermediate segment(s); maxillary palp 7-segmented, extremely slender and about twice as long as the labial palp; 2nd segment about as long as 5th + 6th + 7th; and 5th almost as long as 6th + 7th; distance between antennal sockets more than twice as long as distance from antennal socket to front of clypeus; eyes oval, about one-and-a-half times as long as high and inner orbits subparallel; in dorsal view the eye is one-third longer than the length of the head behind the eyes. *Antenna* 18- to 20-segmented; 1st segment (excluding radicle) and 3rd segment ± equal in length; from 4th onwards each segment decreasing in length and breadth. *Wing* venation with the stigma of the fore wing rather broad (from four to five times longer than broad) and broader than cell C; in the anal cell vein A2 ± fades out before the cross-vein; and vein $2r$ in the fore wing is about one-sixth from the apex of the stigma and is received on RS in front of $2rm$ almost as far as length of $1rm$; and cell $2R_1$ is about three-fifths as long as $3R_1$. *Legs* with hind tarsus longer than tibia; claws each with a strong erect middle tooth; hind claw almost one-and-a-half times as long as middle claw. Saw-sheath about two-thirds as long as basal plate.

Type species: *Xiphydria obtusiventris* Rohwer (Queensland). Distribution: AUSTRALIA and ARU. Other species: *X. leai* Forsius (Queensland), *X. rufipes* Smith (Aru) and *R. wilsoni* sp. n. (New South Wales).

This genus is distinguished from all other Xiphydriinae except *Moaxiphia* Maa by its long 7-segmented maxillary palps (about twice as long as labial palps); the fading out of vein A_2 in the fore wing it also shares with *Moaxiphia* and with *Indoxiphia* Maa. It is distinguished from *Moaxiphia* (into which genus the described species were placed by Maa) by the parallel inner orbits, the broader interantennal area in relation to clypeal length (in *Moaxiphia* the distance between the antennal sockets is very little more than, and much less than twice, the distance between an antennal socket and the front of the clypeus), the longitudinally divided temples behind the eyes and the enlarged hind claws of the female.

Rhysacephala wilsoni sp. n.

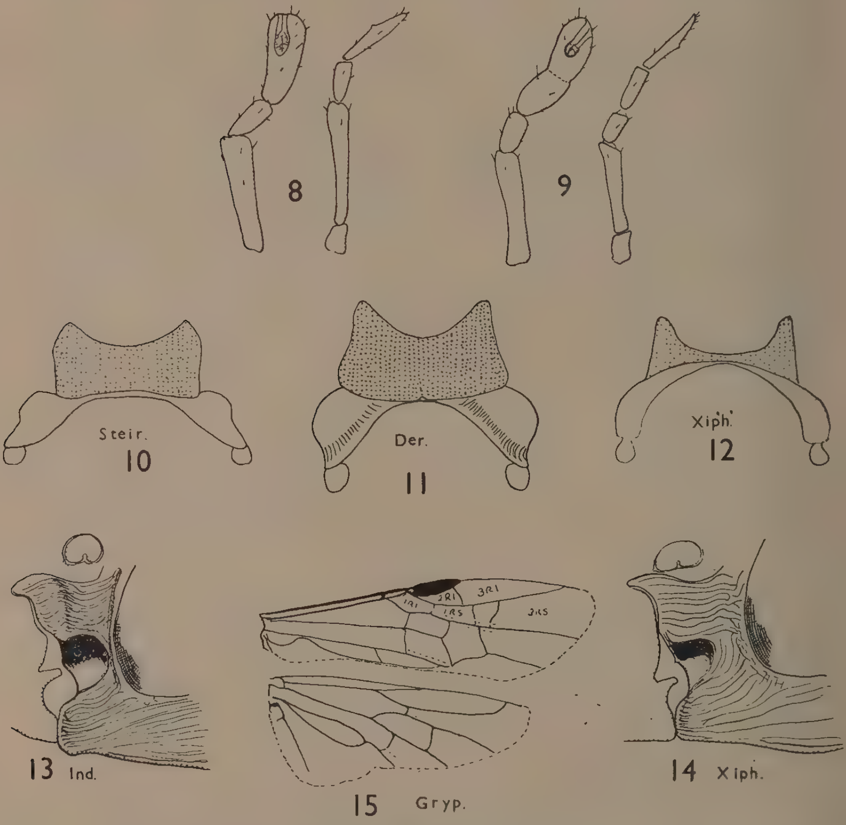
Female.—Black or piceous with the following parts yellow to yellowish brown: mouth-parts, antenna, legs (except the coxae, base of tibae and metatarsi) and ± sides of abdomen; and the following parts white: lateral hind margin of pronotum, tegula, coxae, bases of tibiae and metatarsi, a small fleck on the side of the 1st tergite, a larger fleck on the side of each of the 2nd to 7th tergites, and a large fleck on the 8th tergite covering each side to the length of about a quarter of the tergite. *Wings* hyaline; stigma and venation in apical half of wings piceous but in basal half becoming yellow. *Head* with sculpture on frons coarsely reticulate, the carinae becoming circular close round the antennal sockets; behind the ocelli and eyes densely transversely striate and with a medial longitudinal furrow. *Antennae* (broken beyond 9th and 12th segments). *Thorax* with coarse reticulate sculpture on mesonotum becoming finer near middle line of front lobes and on lateral lobes, and on the middle of the scutellum, which is almost impunctate elsewhere. *Abdomen* with normal transverse coriaceous sculpture; ovipositor about 2·3 mm. long. Length: 10·5 mm.

VICTORIA: Ringwood, 1 ♀ (holotype), 19.xi.1939 (*F. E. Wilson*) (in Mr. Wilson's Collection).

This species is easily distinguished from *R. obtusiventris* (Rohwer) which has no white flecks on the abdomen and in which the sculpture of the frons, though reticulate, is dominated by longitudinal carinae from the ocellar region to the clypeus. In *R. leai* (Forsius) the body is described as being entirely ochraceous to testaceous, without white flecks on the abdomen but with piceous antennae, and a large dark piceous spot on the vertex of the head incised laterally on each side by a longitudinal white stripe. *R. rufipes* (Smith) (Aru), though very similar in colour to the new species, is distinguished at once because the temples behind the eyes are not transversely striate and the medial furrow is broken up into a line of punctures. *R. testacea* Mocsáry (New Guinea) I have not seen, and it may not belong to this genus; it cannot be confused with the present species as it is described as being entirely testaceous, marked with white, and with the temples impunctate behind. *X. laeviceps* Smith (Buru and Amboina), referred by Maa to *Moaxiphia*, belongs really to *Cingalixiphia* Maa (**comb. nov.**).

Cingalixiphia Maa **stat. nov.**

Maa treats *Cingalixiphia* as a subgenus of *Indoxiphia* Maa, distinguished from it only in that vein *rm* is absent in the hind wing, not a convincing character



Figs. 8–15.—(8–9) Labial palp (left) and maxillary palp (right) in two examples of *Xiphydria camelus* to show variation in segmentation. (10–12) Pronotum of: 10, *Steirocephala*; 11, *Derecyrta*; and 12, *Xiphydria*; in each the collar (stippled) is shown in the same plane as the dorsal part. (13–14) Gena to show malar depression and antennal groove in: 13, *Indoxiphia*; 14, *Xiphydria camelus*. (15) Right wings of *Gryponeura*.

and inapplicable to *C. laeviceps* (Smith). I regard *Cingalixiphia* Maa as a distinct genus on the following grounds not mentioned by Maa :

A. Front claws toothed ; middle and hind claws simple. Vein A_2 in fore wing entire. Face sculptured with longitudinal striae in front of ocelli. (Labial palps 3- to 4-segmented ; maxillary 5-segmented) **Cingalixiphia** Maa.

B. Front and middle claws toothed ; hind claws simple. Vein A_2 in fore wing fading out before anal cross vein. Face with coarse reticulate sculpture in front of ocelli. (Labial palp 4-, maxillary palp 5-segmented) . . . . **Indoxiphia** Maa.

Xiphidiaphora gen. n.

Belongs to Xiphydriinae as defined above.

Head about as wide as thorax and slightly narrowed behind the eyes, where the temples are about as long as the length of an eye in dorsal aspect ; malar space from eye margin to inner edge of malar depression very short (as in fig. 13) ; clypeus together with interantennal area longitudinally striate ; frons reticulately punctured ; ocellar region with radiating striae ; postorbital area smooth and impunctate except medially in front ; genal and occipital carinae well defined ; labial palp 3-segmented ; the 3rd segment dilate but acuminate apically ; 1st about as long as 2nd + 3rd ; maxillary palp (broken) ; distance between antennal sockets about twice the distance between an antennal socket and the front of the clypeus ; eyes oval (length to height about 1·0 : 1·2) ; inner orbits diverge above ; antenna 16-segmented, about one-and-a-half times as long as width of head behind the eyes. *Thorax* with very coarse transverse-reticulate rugae and carinae on the mesonotum ; scutellum coarsely reticulate above, rugose and finely reticulate at sides, impunctate behind ; mesosternum coarsely reticulate. *Legs* with hind tarsus about equal to tibia ; tarsal claws strongly curved, and with a long medial tooth almost as long as the end tooth, as well as a slight basal lobe. *Wings* with vein 2*r* missing in fore wing and *rm* in hind wing ; otherwise as in *Xiphydria camelus* L. *Abdomen* coriaceous all over except at the base of some of the basal tergites, the apical depressed parts of which are more coarsely punctured.

Type species : *Xiphydiaphora erebus* sp. n.

This genus is distinguished from all other genera in the Xiphydriinae by the absence of vein 2*r* in the fore wing. It is probably most closely related to *Hyperxiphia* Maa.

Xiphidiaphora erebus sp. n.

Colour piceous black ; wings hyaline, slightly brownish in apical two-thirds ; stigma brown ; venation brown to piceous. *Antenna* with 1st segment about as long as 2nd + 3rd ; 3rd twice as long as 2nd which is equal to 4th. Ovipositor about 3 mm. ; sawsheath to basal plate as 1·0 : 1·2. Length 14 mm.

INDO CHINA : Tonkin, Chapa, 1 ♀ (holotype), 21.v.1916 (*R. V. de Salvaza*) (in British Museum).

Gryponeura gen. nov.

Belongs to Xiphydriinae as defined above.

Head about as broad as the thorax and subparallel sided ; densely punctured and pubescent above behind the ocular line ; labial palp 3-segmented, with the 3rd segment dilated and about as long as the 1st and three times as long as the 2nd ; maxillary palp very slender, 4-segmented, with the 2nd and 4th segments elongate and equal and the 3rd very short; malar space from eye margin to inner edge of malar depression very short (as in fig. 13); distance between antennal sockets about three times the distance from a socket to the front of the clypeus; interantennal area reticulate with striae predominantly longitudinal; frons shining between punctures, which become coarse and confluent close to orbits, and in ocellar region striae radiate from the ocelli; genal and occipital carinae well defined. Antennae 11- to 12-segmented and about as long as the breadth of the head behind the eyes. *Legs* with hind tarsus longer than tibia (1·8 : 1·0); claws sharp and fine, front and middle pairs almost sub-bifid; hind pair with a long erect middle tooth.

Wings with broad stigma to fore wing (only about four times longer than broad), and compared to related genera there is a definite shift of veins in the apex of the fore wing towards the base of the stigma (fig. 15): vein *2r*, for example, is one-quarter to one-fifth from the apex of the stigma so that cell $2R_1$ is less than half $3R_1$ (1·0 : 2·6); and *2r* is received on RS in front of *2rm* by about the length of *1rm*, whereas *3rm* is curved and very close to *2rm* (about as close or closer to *2rm* above than its own height and from half to two-thirds this below, and the length of cell 3RS is at least as great as $1R_1+1RS$). Ovipositor about as long as hind tarsus with sawsheath and basal plate approximately equal.

Type species: *Xiphydria quadrimaculata* Cameron, 1899, India (Assam: Khassia Hills and Shillong); also includes *X. orientalis* Westwood, 1874, India (Nilgiri Hills) and Ceylon.

By its densely sculptured and pubescent temples this genus is distinguished from all other Xiphydriinae and more resembles *Brachyxiphus* of the Derecyrtinae. *Platyxiphydria*, *Xiphydriola* and *Rhysacephala* (of Xiphydriinae) have more or less densely sculptured temples, but these are almost entirely glabrous. The new genus also differs from all others in the way the venation in the apex of the fore wing has shifted basad so that, for example, cell $3R_1$ is about two-and-a-half times as long as $2R_1$, and 3RS at least as long as $1R_1 + 1RS$. The two species *G. quadrimaculata* (Cameron) and *G. orientalis* (Westwood) can be distinguished by the much longer pubescence on the temples and mesonotum of the latter species (some of it longer than the diameter of a hind ocellus but only a half to three-quarters this length in *G. quadrimaculata*).

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THE EXTERNAL MORPHOLOGY OF *CHIROTHRIPS HAMATUS* (TRYBOM) (THYSANOPTERA).

By Tecwyn Jones, B.Sc., A.R.C.S., F.R.E.S.
(*Imperial College of Science and Technology*).

Manuscript received 20th October, 1953.
(Read 4th November, 1953.)

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INTRODUCTION.

PUBLISHED accounts of the skeletal anatomy of the Thysanoptera disagree considerably over the nomenclature and homologies of the various parts. The present study of the external structure of *Chirothrips hamatus* (Trybom) has been undertaken with a view to examining some of these divergences of opinion and an attempt is made to apply, as far as is possible, the principles developed by Snodgrass (1935, etc.). It is hoped that, in addition to any purely morphological interest it may have, the account will help to provide a more adequate anatomical basis for taxonomic work in this order.

METHODS.

Freshly killed specimens were mounted immediately in polyvinyl-lacto-phenol solution and material which had been preserved in alcohol was dealt with in the same way after gentle maceration in caustic alkali and treatment with acetic acid. The same mountant also proved successful as a dissecting medium. Pigmented structures were bleached with Diaphanol when necessary and acid fuchsin-picric acid staining was used for musculature and sensilla.

ACKNOWLEDGMENTS.

The author wishes to thank Dr. W. F. Jepson, O.B.E., for suggesting this study and Professor J. W. Munro, C.B.E., for kindly providing facilities at the Imperial College of Science and Technology. The manuscript was seen through the press by Mr. R. G. Davies.

1. HEAD.

(a) Head capsule.

The head of *Chirothrips hamatus*, as in all other Thysanoptera, is opisthognathous (or modified hypognathous of Pesson (1951), figs. 10*a* and 10*b*). This condition is due to the large posterior base of the head being attached to the prothorax at an angle and thus causing a deflection of the facial region. This deflection results in the cone-like mouthparts occupying the caudo-ventral portion of the head capsule, projecting downwards and slightly backwards between the bases of the fore legs.

The facial region of the head is generally oblong, having the greatest width just below the eyes (fig. 10*a*). The sides are more or less convex, whereas the face is generally flat. The antennae are inserted on the top of the head—actually on the extreme anterior region—and are almost contiguous. Their bases lie symmetrically on each side of the mid-dorsal line and the rest of the antenna projects straight in front of the head (figs. 10*a* and 10*b*).

A pair of compound eyes is situated on the dorsolateral walls of the cranium (fig. 1) and between them on the dorsal part of the head are three ocelli. These ocelli, which are arranged in a triangle, are present only in the female.

(i) *Surface Areas of the Head.*

In *Chirothrips hamatus* there has been considerable fusion of head sclerites and hence only a few sutures are visible. This makes the task of homologising the various regions with those of the typical insect head exceedingly difficult. Previous workers on other Thysanoptera have put forward various interpretations and in this paper those interpretations most in keeping with the nomenclature of Snodgrass (1935, etc.) have been accepted, with only slight modifications.

(ii) *Cranial Sutures and Plates.*

The dorsal view of the head (fig. 1) shows no sign of a coronal suture nor are frontal sutures visible. This results from the complete fusion of the parietals, frons, etc., and the limits of these various plates can only be determined by a detailed study of internal musculature. One suture, however, which separates a posterior arch from the rest of the head, is visible and this undoubtedly represents the *occipital suture* (Pesson, 1951). The region posterior to this represents the occipital plates (again fused to form a complete arch) and the region anterior to the suture represents the vertex. The subdivision of the vertex will be discussed later.

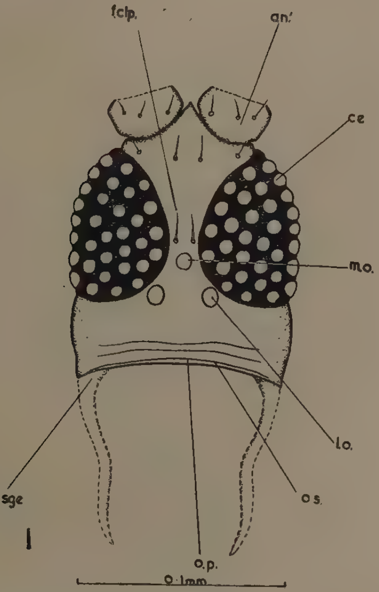

FIG. 1.—*Chirothrips hamatus* (Trybom). Dorsal view of the head of the female. *an*¹, antenna ; *ce*, compound eye ; *f.clp*, fronto-clypeus ; *lo*, lateral ocellus ; *mo*, median ocellus ; *op*, occipital plate ; *os*, occipital suture ; *sge*, subgena.

The facial region (fig. 10*a*) is markedly asymmetrical, particularly in the area adjoining and surrounding the buccal cone. Only two prominent sutures are present, both of which are transverse but inclined in opposite directions so as to enclose between them a wedge-shaped plate (*an. clp*).

The more dorsal of these two sutures (s_1) forms internally a thickened ridge to which is attached the left tentorial arm (*l.tnt*). Pesson (1951) has labelled this suture as a clypeolabral suture but from the attachment of the cibarial dilator muscles it is clear that it represents a transclypeal suture. The plate (*an.clp*) which lies ventral to this suture (s_1) represents a part of the clypeus, whilst the suture limiting the ventral edge of this plate is the true clypeolabral suture (s_2). The asymmetrical sclerite ventral to the clypeolabral suture is the labrum (*lbr*).

The anterior tentorial pits are absent in this species and hence the epistomal suture cannot be traced.

The large facial region dorsal to the transclypeal suture and extending between the compound eyes (*p.clp*) has no subdivisions. Reyne (1927) has labelled this area as frons, but Peterson (1915) and Melis (1933–1935) indicate in their diagrams of other species that the cibarial dilator muscles have their attachments on the inner side of this plate. This fact indicates—on the definition by Snodgrass (1935)—that this area represents part of the clypeus. Furthermore, these workers have shown that the muscle attachments extend dorsalwards beyond the antennae to the region of the median ocellus. Börner (1929) and Weber (1933), from their study of head musclature and frontal ganglia, have supported this interpretation. The facial region then is composed of clypeus only, the frons does not contribute and must be restricted to a small area on the dorsal side of the head. There are no sutures to indicate the extent of the latter region but it is likely that the frons is limited to the area bearing and closely surrounding the median ocellus. Posterior to the frons, the whole dorsal surface of the head represents the parietals, separated only from the occipital ring (*op*) by the occipital suture (*os*). The latter has been labelled as such by Pesson (1951) and as no posterior tentorial pits were found in association with this suture in *Chirothrips hamatus*, there is no reason for regarding it as the postoccipital suture. Peterson (1915) claims that in *Heliothrips* there are posterior tentorial pits and a postoccipital suture is present. There is no distinction in the species studied here between the lateral region of the parietals and the genae (*ge*). The latter occupy a large area below the compound eyes and at the junction of the transclypeal suture and the occipital plate the genal region is extended ventrally to form caudal prolongations. The latter were so named by Peterson (1915), but Pesson (1951) interpretates them as subgenal plates due to the presence of a subgenal suture. The latter suture is present in *Chirothrips hamatus* (*sb.ge.s*) in a less complete form and therefore Pesson's nomenclature has been adopted.

(iii) *The Compound Eyes.*

The compound eyes are large, and occupy a considerable area of the lateral and dorsal region of the head (figs. 1 and 10). This is particularly true in the female, where the eyes extend a considerable way to the mid-dorsal region of the head and thus cause the vertex in this region to become much narrower than in the male. The eye consists of a relatively small number of facets, each of which is large, highly convex and separated from its neighbours by a fairly wide non-faceted area. In living specimens a mass of red pigment is associated with the inner regions of the eye and gives the appearance of greatest concentration on the mesial side.

(iv) *Tentorium.*

In *Chirothrips hamatus* the tentorium (*tnt*) can be clearly seen in macerated specimens without dissection. Externally no anterior tentorial pits could be seen but the main body of the tentorium appears to be closely associated with the thickened border of the postclypeus (fig. 10*a*). The structure is composed of two parts, one on the right side of the head and the other on the left, and each extends dorsalwards to the ventral angle of the corresponding eye. The left tentorial arm (*l.tnt*) is more complete than its partner and on its lateral edge gives rise to a curved prolongation. The main body of this arm probably represents the anterior arm of a much reduced tentorium, whilst the prolongation may be a remnant of the connection between this arm and the posterior arm. The latter is completely absent and no trace of the posterior tentorial pits was observed. The right tentorial arm is even more reduced and does not reach the clypeal border. On both sides the tentorium is fused with the inner walls of the postclypeus.

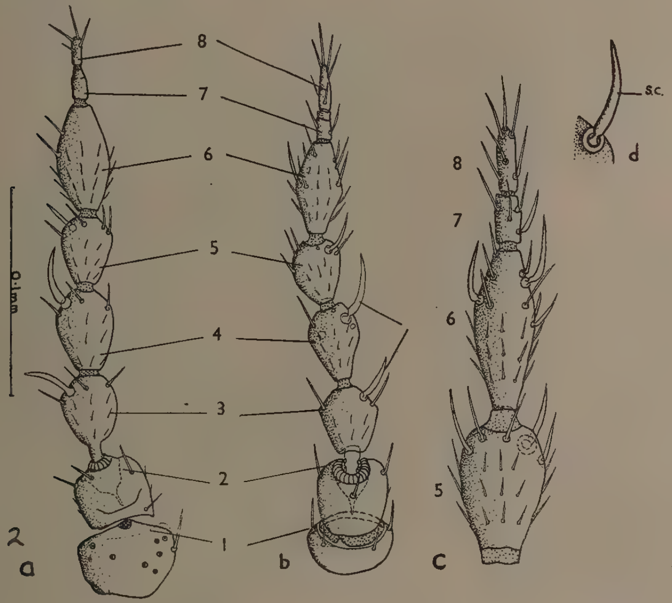

Fig. 2.—*C. hamatus.* (*a*) Dorsal view of the antenna (female). (*b*) Ventral view of the antenna (female). (*c*) Distal end of the antenna. (*d*) Sense cone of antenna. Nos. 1 to 8—antennal segments; *sc*, sense cone.

(b) Head Appendages.

(i) *Antennae.*

The antennae (figs. 2*a* and 2*b*) are situated on the extreme anterior margin of the head capsule. Their bases are separated by a small triangular projection of the cranium. In form they are more or less moniliform and in this species consist of eight segments, the distal three of which taper so as to form a stylus.

The third and fourth segments possess distinct *sense cones* (2*d*, *s.c.*) each with a definite articular cup. A similar sense cone is present on the fifth segment, but here it is less well developed.

(ii) *Mouthparts.*

The mouthparts together form the so-called buccal cone which is markedly asymmetrical (figs. 10*a* and 10*b*).

Labrum.

The labrum consist of an asymmetrical plate which forms the anterior or upper lip of the buccal cone (fig. 5). It extends further dorsalwards and laterally on the right side than on the left and meets the anteclypeus (*an.clp*) at the clypeolabral suture (S_2) along its whole proximal edge. The extreme right external angle of the labrum ((x^1) appears to articulate with both the ante- and postclypeus (fig. 10*a*). The labrum itself is not a simple plate but three distinct regions, a fact which has led many workers, e.g., Melis (1935), to assume it represents a clypeolabrum. The main plate is the large asymmetrical heavily sclerotised area which bears five spines (fig. 5, *ch.p.lbr*). Distal to this is a membranous area bearing a single spine and, unlike the more proximal region, not highly convex. The line of separation of these two regions (*s*) is well marked and was assumed by some authorities to represent a suture, but it appears to be nothing more than the limit of heavy sclerotisation of the labrum. The membranous region changes abruptly into a cup-shaped structure (*lbr.c*), with heavily sclerotised longitudinal bands. This symmetrical structure —the distal end of the labrum—is highly convex and freely movable, due to the flexibility of the membranous region at its base. It has been labelled here as the labral cup but actually it is more in the form of a half-cylinder or inverted trough. The function of the cup is quite obviously to direct and hold firmly the maxillary and mandibular stylets, together with the distal end of the maxillary lobe. This function is aided by the presence on the inner ventral side of the labrum of a trough shaped structure (*s.d.p*) (fig. 5). This structure—the " styli del palato " of Melis (1935)—appears from dissection to be composed of two separate but closely associated sclerotisations. Its attachment to the inner wall of the labrum by a membrane and not by fusion, indicates that it does not represent a true epipharynx. It has been regarded by Reyne (1927) and by Snodgrass (1935) as the sclerotised dorsal wall of the cibarium. Pesson (1951) agrees with this and states that the muscles pertaining to these structures have their attachments on the tentorium.

Mandible.

The adult *Chirothrips hamatus* has only one complete and fully functioning mandible. This left mandible (fig. 3) does not partake in the surface area of the buccal cone and hence is not visible externally. Its presence internally causes a slight displacement of the maxilla. The mandible consists of a heavily sclerotised stylet (*st*) which passes abruptly into a wider basal part (*mb.st*). This more membranous basal portion articulates with the head capsule in the region of the left external angle of the clypeolabral suture by means of a short condyle (*cnd*). The latter is borne on a heavily sclerotised rim (*ch.r*). The stylet itself is thicker than that of the maxilla and appears to possess a longittudinal canal (*ax.c*) which reaches almost to its distal end.

The right mandible is much reduced and is represented only by a vestige of the basal region. It is situated in the right proximal angle of the anteclypeus and is fused with the latter. There is no evidence in favour of Reyne's interpretation that this structure represents an apodeme rather than a reduced mandible.

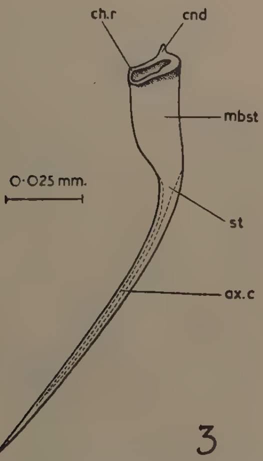

Fig. 3.—*C. hamatus*. Anterior view of the left mandible. *ax.c*, axial canal ; *cnd*, condyle ; *ch.r*, sclerotized rim ; *mbst*, membranous base of stylet ; *st*, stylet.

Maxillae.

The two maxillae are well developed and represent the main piercing organs. They occupy the lateral area of the buccal cone, between the labrum and the labium and articulate at their bases with the subgenal plates (fig. 4). Each maxilla consists of a long mesal stylet (*st*) which is linked to a less strongly sclerotised external lobe (*mx.l*) by a lever (*lv.*). The maxillary lobe, which forms the lateral regions of the buccal cone (fig. 10*b*) bears on its outer edge a three-segmented maxillary palp, the distal segment of which is less sclerotised and more freely movable than the proximal segments. The lobe narrows towards its distal end and at its extremity becomes slightly bulbous. This latter region bears two or three spines (*sp*) which normally project laterally (i.e., horizontally) and are probably sensory (fig. 4). The lateral proximal region of the maxillary lobe bears a short but distinct condyle (*cnd*) which articulates with the subgenal region of the head. Arising from the mesal proximal region is the lever, attached to the distal end of which is the stylet. The region bearing the palp is less membranous than the rest of the lobe and distally, below the palp, are a small number of broad, minute spines. The rest of the lobe is more heavily sclerotised and bears two large spines.

The lever extends inwards and further dorsalwards than the maxillary lobe

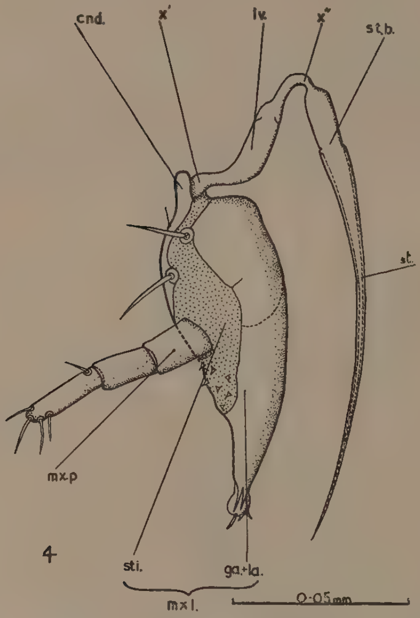
cnd.
x′
lv.
x″
st.b.
st.
mx.p
4
sti.
ga.+la.
mx l.
0·05 mm

FIG. 4.—*C. hamatus.* Anterior view of the right maxilla. *cnd*, condyle; *ga* and *la*, galea and lacinia; *lv*, lever; *mx.l*, maxillary lobe; *mx.p*, maxillary palp; *st.b*, base of stylet; *sti*, stipes; *st*, stylet; *x′* and *x″*, points of flexure.

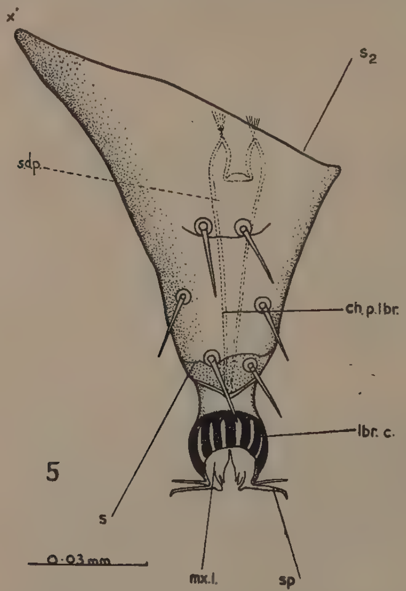
x′
S_2
s.d.p.
ch.p.lbr.
lbr. c.
5
s
0·03 mm
mx.l.
sp

FIG. 5.—*C. hamatus.* Dorsal (facial) view of the labrum. *chp.lbr*, sclerotized part of labrum; *lbr.c*, labral cup; *mx.l*, maxillary lobe; S_2, clypeolabral suture, *S*, end of sclerotisation; *s.d.p.* sclerotised dorsal cibarial wall; *sp*, spines; *x′*, labral angle.

and allows flexure at two points (x' and x'') (fig. 4). There is no true articulation where the lever joins the broad fleshy base of the stylet, merely a line indicating probable fusion of the two parts. The base of the stylet curves ventrally and after a short distance changes abruptly to the heavily sclerotised stylet and this continues ventrally and projects through the labral cup.

The maxilla, then, is highly modified and in appearance is quite different from that of the primitive insect. Reyne (1927), Pesson (1951) and Snodgrass (1935) have indicated possible homologies. Reyne showed that the stylet arises in the embryo by splitting off from the main body of the maxilla. Pesson, from consideration of this and work by Buffa (1898) and Peterson (1915), has concluded that the lever represents the *cardo*; the membranous area of the lobe represents the *stipes and palpiger* (*sti*), whilst the distal end represents the fused *galea and lacinia* (*ga* and *la*). (In *Chirothrips hamatus*, however, this fusion may not be as complete as in most Terebrants as there is a slight indication of unequal lobes at the distal end, but they may of course be secondary). Snodgrass (1935) regards the stylet as a cuticular spine produced from the mesial part of the lobe and secondarily split off from the region of cardo and stipes.

Labium.

This appendage, unlike the rest of the mouthparts, is bilaterally symmetrical. It is highly convex and composed of two main sclerites separated by a well marked suture (*s*) (figs. 6*a* to 6*e*). The basal plate (*pm*) is simple, and forms an attachment with the genal region of the head capsule. The distal plate (*pr.m*) is differentiated into a basal sclerotised portion and a pair of membranous lobes (*me*), and this whole structure is curved so as to present a pair of lateral infoldings on the anterior (i.e., dorsal) side of the labium. Each lobe bears a single unjointed labial palp (*plp*) and ends in a number of small cylindrical processes, each of which bears a sensory hair at its extremity. In addition, on the mesal side of each lobe is a small sclerotisation (*sp*), the sensory plate of Pesson (1951).

The homologies of the various sclerites are uncertain but the nomenclature adopted here depends on the definitions of Snodgrass (1935). The distal plate (*prm*) is termed the prementum because it bears distally the labial palps. The proximal (*pm*) plate has been labelled as *postmentum*, which it must be if the other interpretation is correct. Reyne (1927) has labelled the proximal plate as submentum and the distal plate as mentum, but this cannot be correct as the mentum never bears the palps (Snodgrass 1935). It is possible that the proximal plate represents the submentum, the distal plates the mentum and the membranous area bearing the palps is the prementum. This interpretation, however, would necessitate (on definition) that the muscles controlling the palps should be attached to the membranous area, a condition that has not been described or illustrated in any Terebrantia. Thus, until such evidence is found, this latter interpretation cannot be accepted without reserve, and judging from the lack of apparent means of attachment of such muscles to the membrane it seems rather unlikely that it is correct. The interpretation given in this paper is correct in so far that the plate labelled prementum must contain the prementum at least, as proved by the palps. Whether the prementum is fused with the mentum is, of course, open to question and can only be decided on the basis of the musculature.

The labial palps consist of one apparent segment and a small basal piece, and the latter represents either a second segment or the *palpiger*. This fact can only be decided by musculature.

The complex membranous lobes (*pgl*) are here interpreted as the paraglossae, in agreement with the work of Pesson (1951) and Melis (1935) on other species.

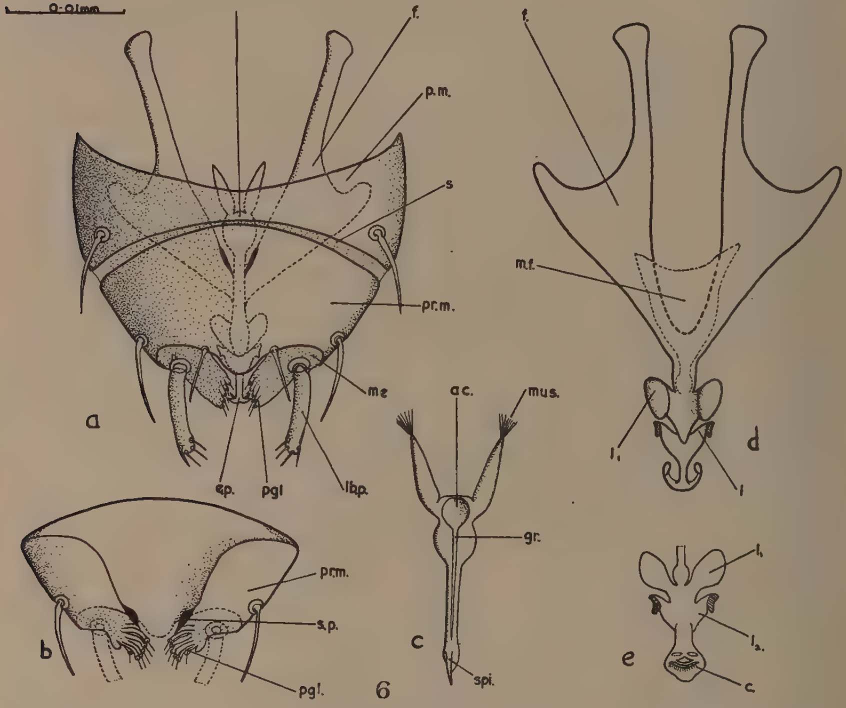

Fig. 6.—*C. hamatus.* (*a*) Ventral (posterior) view of labium. *ep*, end piece of hypopharynx; *f*, fulturae; *lb.p*, labial palp; *me*, membrane; *pgl*, paraglossae; *pm*, postmentum; *pr.m.* prementum; *s*, suture. (*b*) Dorsal (anterior) view of prementum. *p.gl*, paraglossae; *pr.m*, prementum; *sp*, sclerotised sense plate. (*c*) Dorsal view of the salivary pump. *ac*, axial canal; *gr*, groove; *mus*, muscle; *spi*, spine. (*d*) Ventral view of the hypopharynx. *f*, fulturae; l_1 and l_2, lobes; *mf*, membranous flange. (*e*) Distal end of hypopharynx, dorsal view. *c*, comb; l_1 and l_2, lobes.

No glossae were observed in *Chirothrips hamatus* but this deficiency is not entirely unexpected as the area between the paraglossae is occupied by the highly complex distal end of the hypopharynx.

The hypopharynx and associated structures are shown in fig. 6. Particularly noteworthy are the greatly developed fulturae and the lobe-like processes in which the hypopharynx ends distally.

2. THORAX.

The thorax is basically similar in both sexes. The differences in size, and relative proportions of the thoracic segments are correlated with the apterous and alate conditions of the male and female respectively.

(i) *Female Thorax.*

In this sex there is a marked secondary division into a distinct prothorax and a compact pterothorax (figs. 11 and 12).

Prothorax.—This segment articulates freely with the head but no cervical sclerites are present. The notal region is composed of one large convex plate, the pronotum (n_1). The pleura are represented by a wedge-shaped sclerite (epm_1) which extends the whole length of the prothorax and is separated from the pronotum by a distinct suture. Midway along this pleural sclerite is situated a thickened ridge (pls_1) with which the coxa of the foreleg articulates. Now by definition (Snodgrass, 1935) this articulatory ridge indicates the position of the pleural suture, and thus the portion of the pleural sclerite anterior to the ridge is the episternum, whilst the portion posterior to the ridge is the epimeron. The interpretation of Doeksen (1941) and Melis (1936) that the pleural sclerite represents the epimeron only, cannot be correct in the light of this pleural suture. The small sclerites which they regard as episterna and which lie ventral to the pleurae represent a part of the sternum (see eps_1). The sternal region consists mainly of membrane. There is, however, a less membranous area (st_1) which may be a remnant of the sternal sclerotisation. This sternal sclerite is continued posteriorly as a thickened projection which articulates with the mesosternum (pst_2).

Pterothorax.—The notal region of the combined meso- and metathoracic segments is composed of three large convex plates and a narrow anterior sclerite. The latter (*acr*), which has a thickened posterior edge corresponding to its inward projection, is the acrotergite of the mesothorax. Posterior to the acrotergite lies the mesonotum which is composed of the fused prescutum and scutum ($psc + sc_2$), a slightly demarcated scutellum (sct_2) and a distinct postnotum (*pn*).

The metanotum consists of two plates each of which is equal in size to the mesonotum. The more anterior sclerite represents the prescutum and scutum (sc_3), whilst the posterior sclerite represents only the scutellum (sct_3). The latter, which overlaps the anterior end of the first abdominal segment, is simple in outline, whereas the scutum possesses lateral projections associated with the wing sclerites.

The mesosternum (st_2) consists of a narrow presternum (pst_2), a large basisternum (st_2) and a posterior sternellum (stl_2). The presternum articulates with the sternal region of the prothorax, whilst the sternellum articulates with the metasternum. The suture between the sternellum and basisternum is represented internally by a ridge which, in the mid ventral line, gives rise to the mesothoracic furca. Laterally the ridge is continued slightly beyond the limits of the mesosternum and thus provides the sternal articulation for the second coxae (cx_2). The coxal cavity, which is covered by membrane, is enclosed between the basisternum and the coxa.

The metasternum (st_3) is a large convex sclerite which extends a considerable way laterally. This latero-dorsal extension is increased by the fusion of the sternal plate with the meta-episternum (eps_3). There is no clear subdivision of the metasternum and as the furca (f) appears to arise from the extreme posterior edge of the sternum there is no evidence of a sternellum. Furthermore, there is no sternal articulation for the third coxae (cx_3) and only a small coxal cavity is present.

The pleural regions of the pterothorax are complex but the very evident pleural sutures facilitate interpretation. The mesopleural suture (pls_2) runs in a straight line from the coxal articulation to the point of articulation of the fore wing. Anterior to this suture are the episternal plates which are represented by a pre-episternum ($pepst_2$) and an episternum ($kepst_2$ and $aneps_2$). The former is a large convex plate and bears on its inner side the mesothoracic spiracle. The episternum is subdivided into a ventral katepisternum ($kepst_2$) and a more dorsal anepisternum ($aneps_2$). Posterior to the mesopleural suture is the meso-epimeron ($kepm_2 + anepm_2$) which is also divided into katepimeron ($kepm_2$) and anepimeron ($anepm_2$). This latter sclerite is characteristically striated and is in close association with the base of the wing processes (wp) and also with the metathoracic spiracle (sp_3).

The metapleura are considerably smaller than the mesopleura. The pleural suture indicates, together with the coxal articulation, that the meta-episternum (eps_3) is fused with the metasternum (st_3). This fusion is not complete in the coxal region, however, and here the episternum is distinct. The meta-epimeron (epm_3) is well developed.

(ii) *Male Thorax.*

Here certain modifications and reductions have resulted from the apterous condition of this sex. The notal region, for example, shows no mesoscutellum and the metascutellum has fused with the metascutum. In the pleural region the mesothoracic katepimeron ($katepm_2$) is subdivided.

The pteralia are naturally reduced and if present are either completely membranous or incorporated into the tegula (*teg*). The latter is thought to be the vestige of the wing base and its articulatory sclerites but Priesner (1949) interprets it as a wing rudiment and thus regards the male *hamatus* as brachypterous rather than apterous.

(iii) *Spiracles.*

Two pairs of thoracic spiracles are present in both sexes, one on the mesothorax (sp_2) and one on the metathorax (sp_3). The external aperture is elaborate in that it possesses a delicate funnel. The walls of this funnel, which connect the sunken atrium with the body surface, are lined with numerous small spherical structures.

(iv) *Thoracic Appendages.*

Legs.—The legs in the male and female are well developed and no secondary sexual characters are present in the male. Each appendage consists of a coxa, trochanter, femur, tibia and a two-segmented tarsus. The distal tarsal segment bears a protrusible bladder.

The fore legs (fig. 7*b*) are shorter and stouter than either of the more posterior pairs, and are carried in life with the tibia parallel to the side of the head. The coxa (*cx*) articulates with the pleural plate (*s*) of the prothorax and appears to be hinged only at this point; no sternal articulation is present. Distally the coxa articulates with both the trochanter (*tro*) and the femur (*fem*). In the case of the latter, the coxa merely projects into a basal cavity of the femur but definite processes are present for the trochantal articulation (fig. 7*b*).

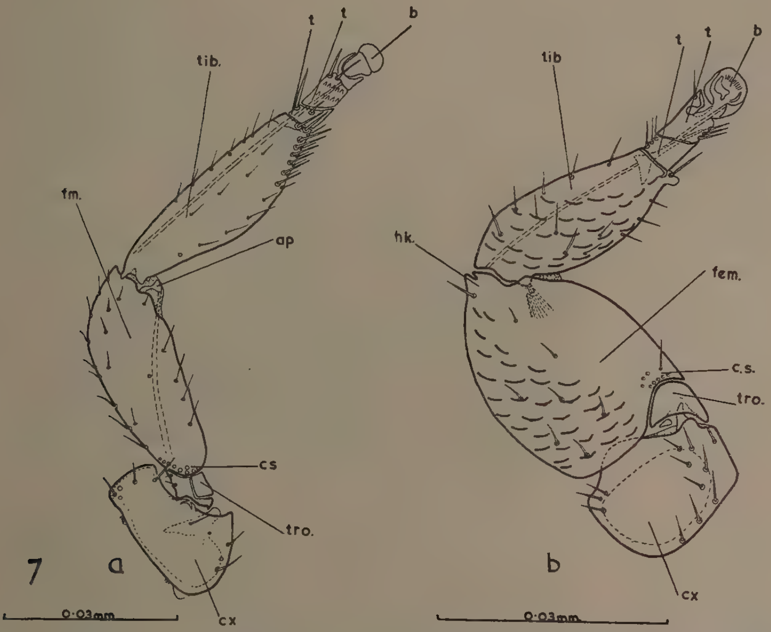

FIG. 7.—*C. hamatus.* (*a*) Ventral view of the hind leg of the female. *ap*, apodeme; *b*, bladder; *cs*, campaniform sensilla; *cx*, coxa; *fm* and *fem*, femur; *hk*, hook; t_1 and t_2, tarsal segments; *tro*, trochanter. (*b*) Dorsal view of the fore leg of the female Lettering as in fig. 7(*a*).

These processes are in the form of a coxal spine, which projects into a groove on the trochanter, and a trochantal spine which does likewise with the coxa. The femur is a large conical segment and bears a characteristic curved pointed tooth at its external apical angle (*hk*). In the region of articulation with the trochanter a small number of campaniform sensilla are present on the femur. The tibia is simple and articulates distally with the basal tarsal segment (t_1) which is markedly asymmetrical. The last tarsal segment (t_2) is highly complex and bears two unequal claws, between which lies the protrusible bladder. Pesson (1951) regards this bladder as a modified arolium, the movements of which are controlled by muscles within the tibia. Such muscles are present in *Chirothrips hamatus* and are connected to the arolium by a tendon which traverses the whole tarsus.

The middle legs are more elongate than the anterior pair but in most respects there is a great similarity. The coxal articulation, however, is more complete as sternal and pleural articulations are present. As a result of this the coxa is movable only in one plane but the trochanter articulates more freely with the coxa than in the fore leg and thus the movement of the appendage as a whole is not restricted. Another consequence of this sternal articulation in the mesothorax is the presence of a well-defined coxal cavity. The latter is covered with membrane and the only trace of a trochantin is a small sclerotised area near the sternal border of the cavity.

The hind legs are almost exact replicas of the mid-legs but on dissection only a pleural articulation was apparent. Staining with picric acid and acid fuschin shows, however, that there are two small areas of sensory hairs—i.e., sense plates—on the coxa. One sense plate is associated with the pleural articulation, whilst the second is situated on the inner sternal angle. This may indicate sternal articulation even though no articulatory processes are present.

Pteralia.—These small plates (fig. 12*b*) are situated between the meso- and metapleura and the corresponding notal regions. Pesson (1951) has attempted to homologise these sclerites with those of less specialised insects and his interpretation has been followed with slight modification.

In the mesothorax there is an anterior humeral plate (*hp*) articulating with the anterior edge of the wing base. Posterior to this lie the axillary sclerites (pt_1 pt_2 and pt_3), the first of which articulates with the dorsal wing process and the base of the radial and cubital veins. The second and third axillaries are associated with the anal lobe of the fore wing. Anterior to the attachment of the wing is situated a triangular tegula (*teg*) which bears a small number of spines on its posterior border. No median plates or subalary sclerites were observed.

The pteralia of the metathorax are reduced and membranous, being represented only by a large " wing process " (*wp*), the homologies of which are not clear.

Wings.—The wings are subequal in length, but the fore wing is broader and stronger than the hind wing. Both are covered with microtrichia (*mi.tr.*) and carry a fringe of long setae on their anterior and posterior borders. Each seta arises from an articulatory socket. In optical section each wing is seen to possess, along the length of the veins, a series of oval lacunae which may represent air cavities. The anal lobe or jugum is well developed in both fore and hind wings.

The venation is much reduced but in the fore wing both a radial and a cubital vein are present. Basally these are combined, but more distally the cubitus is given off as a branch of the radius. The latter extends almost to the extreme distal end of the wing. The presence of a short series of lacunae along the anterior border of the fore wing may be an indication of a costal vein. The radius is the only vein present in the hind wing.

Wing Coupling.—When extended the wings are coupled by means of 4 or 5 curved spines on the costal margin of the hind wing (*wc*) which fit into the anal lobe of the fore wing. The two large spines on the anal lobe of the fore wing (*wc*) probably aid this coupling

3. Abdomen.

(i) *General.*

The abdomen in both sexes is elongate, cylindrical and composed of eleven segments (figs. 14*a* and 14*b*). The attachment with the metathorax is by membrane and the first abdominal segment is partially enclosed by the thoracic sclerites.

Each segment typically consists of a large convex tergum (*t*), a large convex sternum (*st*) and two pairs of pleural sclerites (*p.tr*). The latter have been subject to two interpretations. Melis (1936) labels them as pleurotergites due to their incomplete separation from the terga. The presence of the anterior abdominal spiracles on these *lateral sclerites* and the presence of the posterior spiracles on the eighth *tergum* (where the pleural sclerites are absent) may add weight to this idea. Pesson (1951), on the other hand, regards them as true pleurites and thus implies that the primitive condition has been retained in the abdomen. This implication, however, is difficult to accept in view of the great degree of specialisation in other regions of the body that has occurred in both this species and all other Thysanoptera.

The first segment in male and female is atypical in that it possesses only one pair of pleurotergites and bears the spiracles. Segments two to seven (inclusive) are typical and very similar in both sexes, with the exception that the male possesses large oval glandular areas (*gla*) on the sterna of segments three to seven (inclusive). The presence of the posterior spiracle on segment eight is a feature common to male and female.

The general structure and appearance of the four posterior segments differs markedly according to the sexual organs and will be described separately below.

(ii) *Female.*

The modifications associated with the genitalia involve segments eight to eleven inclusive. In all these segments the sterna are completely membranous and pleurotergites are absent. The terga of segments eight, nine and ten are much enlarged so as to enclose the ovipositor when the latter is retracted. The ovipositor valves arise, one pair from each segment, from the sternal region of the eighth and ninth segment (fig. 15*a*). The eleventh segment is much reduced.

(iii) *Male*

The eighth segment is not associated with the genitalia and hence is complete. The ninth tergum and sternum are much enlarged and form a posterior cone which encloses the retracted genital organs (fig. 8). The sterna of segments ten and eleven are membranous.

4. Genitalia.

(i) *Female.*

The ovipositor is well developed and heavily sclerotised (figs. 14*a* and 15*a*). When protruded it is seen to consist of two pairs of valves closely associated so as to enclose between them an egg canal. When retracted the whole structure is drawn upwards and applied to the membranous sterna of the three posterior segments.

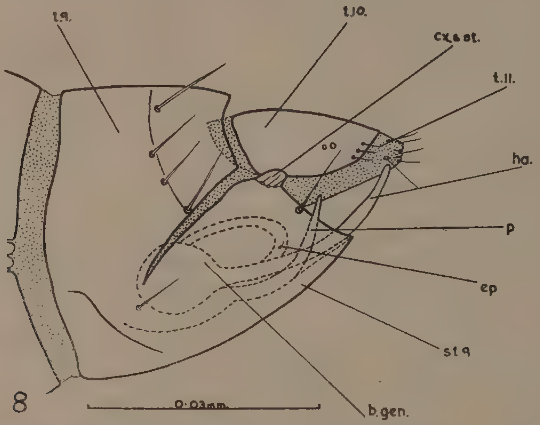

Fig. 8.—*C. hamatus.* Lateral view distal end of male abdomen. *b.gen*, base of genitalia: *cx* and *st*, coxite; *ep*, epiphallus; *ha*, hypophallus; *p*, penis; st_9, 9th sternum or hypandrium; t_9, t_{10}, t_{11}, terga of segments 9, 10 and 11 respectively.

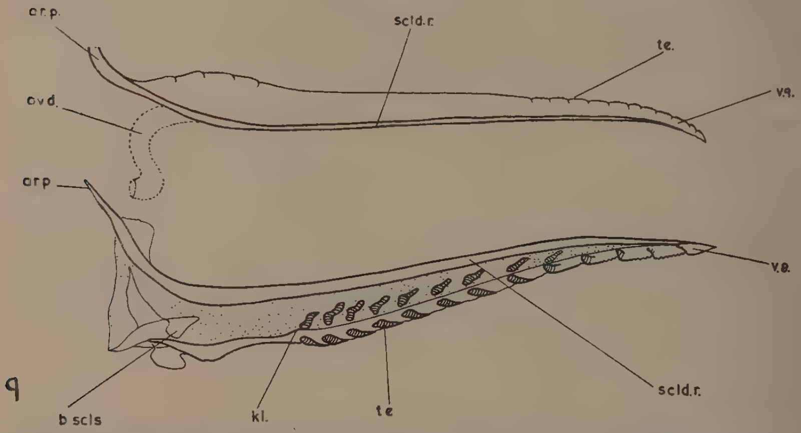

Fig. 9.—*C. hamatus.* Ovipositor valves. *arp*, articular process; *bscls*, basal sclerites; *kl*, keel; *ovd*, oviduct; *scld.r*, sclerotised rim; *te*, teeth; *v8*, valve of 8, *v9*, valve of 9.

The anterior valves (*v*8) which arise from the ventrolateral edge of the eighth sternite articulate proximally with the basal plates (*valf* 8) before continuing internally as an apodeme (*ap* 8). The latter appears to be attached to the anterior edge of the ninth tergum. The three basal plates are enclosed in one mass which forms a definite articulatory structure.

The posterior valves (*v*9) issue from the ventral edge of the ninth sternum.

Each valve is continued internally as a curved rod which articulates with the anterior edge of the triangular sclerite (*vlf* 9). Arising from the dorsal posterior edge of this sclerite is a large apodeme (*ap*9) which is fused along its whole length with the ninth tergum.

The valves themselves are highly complex (fig. 9), being heavily sclerotised on their inner edges (*scld.r*). The outer edges or "keels" are less heavily sclerotised but possess a series of teeth. These teeth are particularly well developed in the anterior valves (*te*), whereas in the posterior valves they are reduced to small serrations. When closely applied the posterior valves fit into the anterior pair and hence are not sheathing.

With regard to the homologies of the components of the ovipositor it is apparent that one pair of valves must be absent by comparison with the primitive insectan condition. The similarities with a Heteropteran condition, e.g., *Anasa tristis* (De Geer) (Tower, 1913) where the third valves are completely lost, allows the interpretation that the basal plates (*valf* 8) and the triangular sclerite (*vlf* 9) represent the first and second valvifers respectively. The valves of segment eight and those of segment nine represent the first and second valves respectively. The absence of the sheathing character of the second valves and the fact that they arise from the anterior edge of the valvifer indicates that they represent the true second valves. The third, sheathing, valves have been lost.

(ii) *Male.*

The male genitalia (figs. 8, 14*c*, 14*d*, 15*c*, 16*a* and 16*b*), together with the infolded terga of segments ten and eleven, are enclosed in the enlarged sclerites of the ninth segment. The sternum of the latter forms the hypandrium and at its dorsal posterior angles bears a pair of small lobes (*cx* and *st*). These lobes represent the reduced coxites, the stylets of which are absent.

The genitalia form a compact mass which is capable of protrusion and retraction. Although complex in appearance the basic structure is quite typical, consisting of a median penis (*p*) and two sets of valves (*ep* and *hph*). The latter are attached to a large sclerotised periandrium (*pa*) at the base of the penis. This structure is interpreted by De Gryse and Treherne (1924) as representing the invaginated tenth sternum. The main body of the periandrium consists of two fenestrated flat plates each with a posterior arch-like prolongation (*p.pa*), and with an anterior dorsal condyle (*cnd*). The penis valves together constitute the periphallus and basally they appear to articulate with the pericardial condyles. The periphallus is composed of the epiphallus (*ep*) and the hypophallus (*hph*), respectively dorsal and ventral to the penis. The epiphallic valves are two in number, and in this species elongate, membranous and recurved on themselves to form a complete ellipse. The hypophallus also consists of two valves. They are well developed, broad basally, and tapering distally, and project just beyond the hypandrium. The dorsal hypophallic valves are absent in this species.

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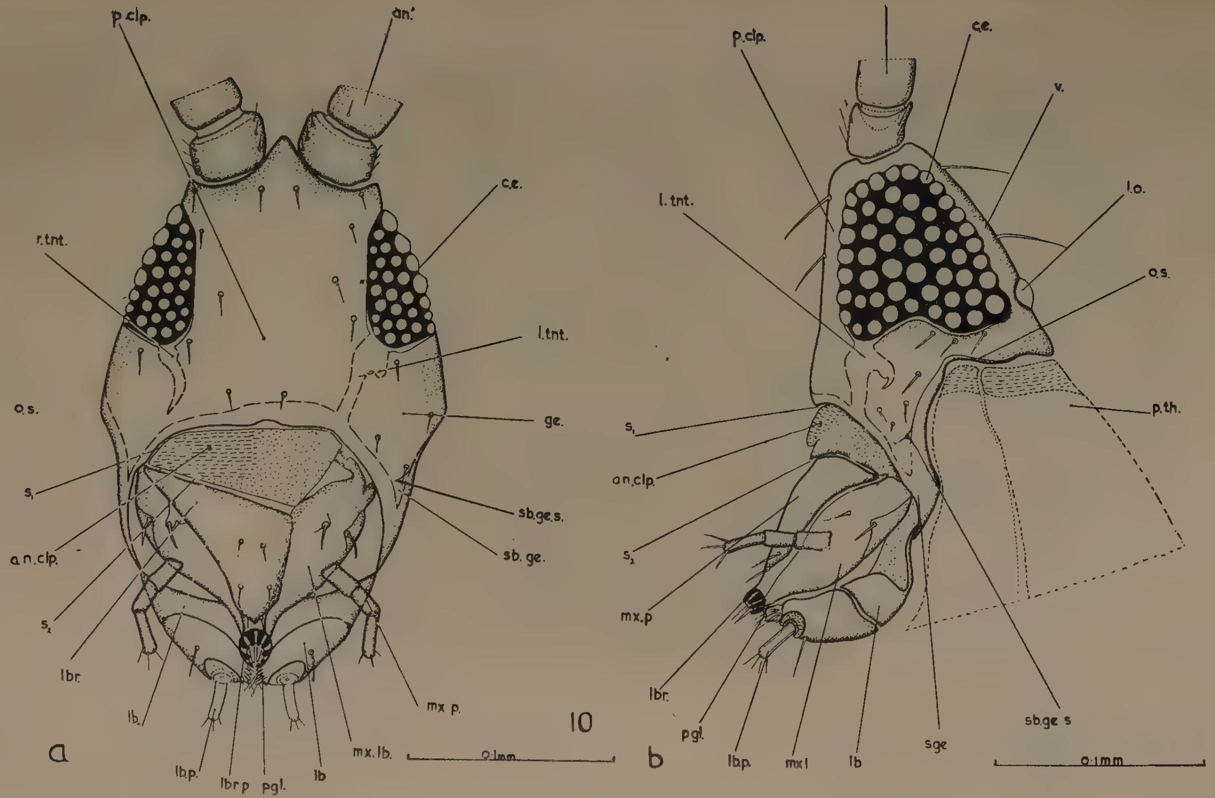
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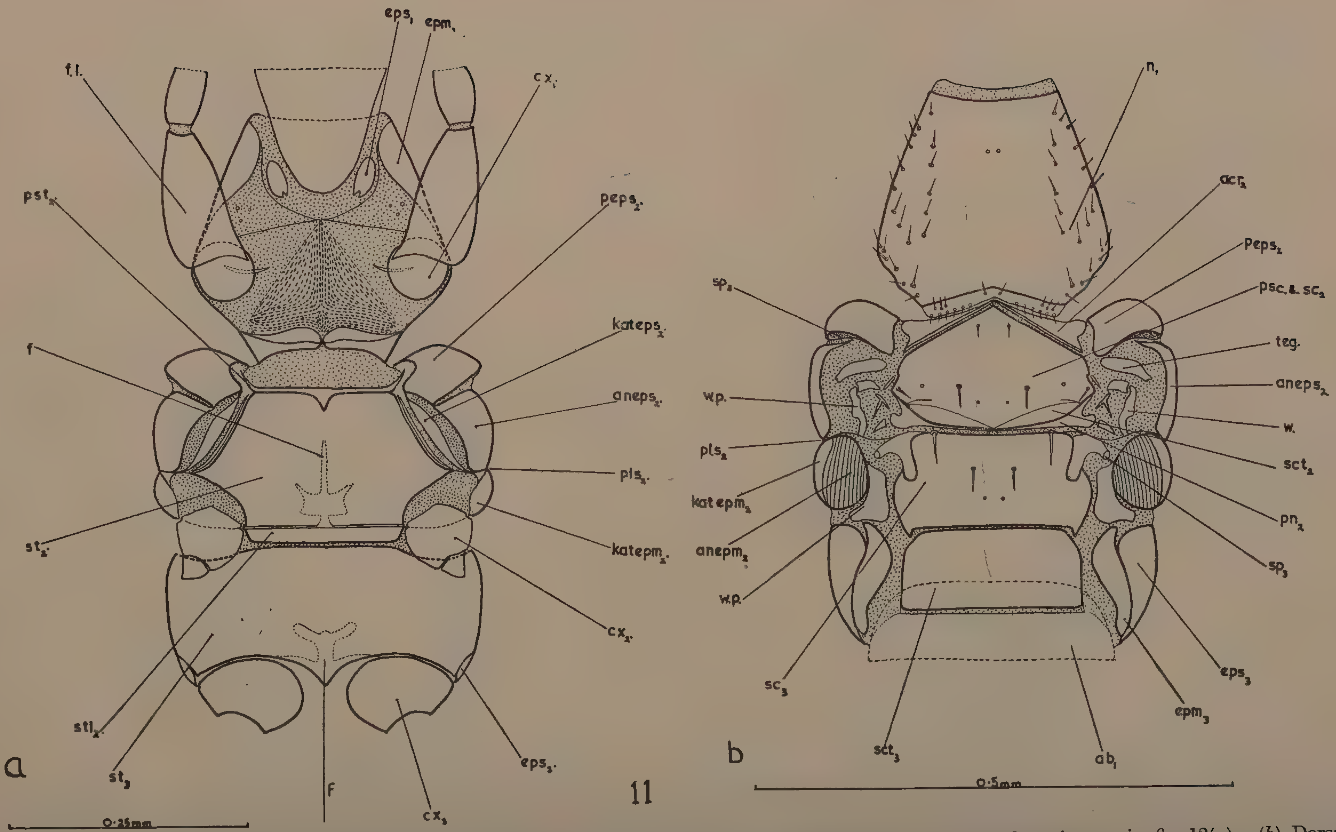
FIG. 10.—*C. hamatus.* (*a*) Facial view of the head of the female. *an*¹, antenna; *an.clp*, ante-clypeus; *ce*, compound eye; *ge*, gena; *lb*, labium; *lbp*, labial palp; *lbrp*, labral cup; *lbr*, labrum; *l.tnt*, left tentorium; *mx.lb*, maxillary lobe; *mx.p*, maxillary palp; *os*, occipital *suture*; *p.clp*, post-clypeus; *p.gl*, paraglossa; *r.tnt*, right tentorium; s_1, transclypeal suture; s_2, clypeolabral suture,; *sb.ge.s*, subgenal suture; *sb.ge*, subgena. (*b*) Side view of the head of the female. *lo*, lateral ocellus; *mx.l*, maxillary lobe; *p.th.* prothorax; *sge*, subgena; *v*, vertex. Other lettering as in fig. 10(*a*).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sct₃
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epm₃
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11

FIG. 11.—*C. hamatus*. (*a*) Ventral view of the female thorax. *f*, furca; *fl*, fore leg; *stl*, sternellum. Other lettering as in fig. 12(*a*). (*b*) Dorsal view of the female thorax. *ab*, abdomen; *acr*, acrotergite; *peps*, pre-episternum; *n*, pronotum; *w*, wing articulation. Other lettering as in fig. 12(*a*). The small suffixes 1, 2 and 3 indicate prothorax, mesothorax and metathorax respectively for figs. 11, 12 and 13. E.g., eps_1, episternum of prothorax; epm_3 epimeron of metathorax.

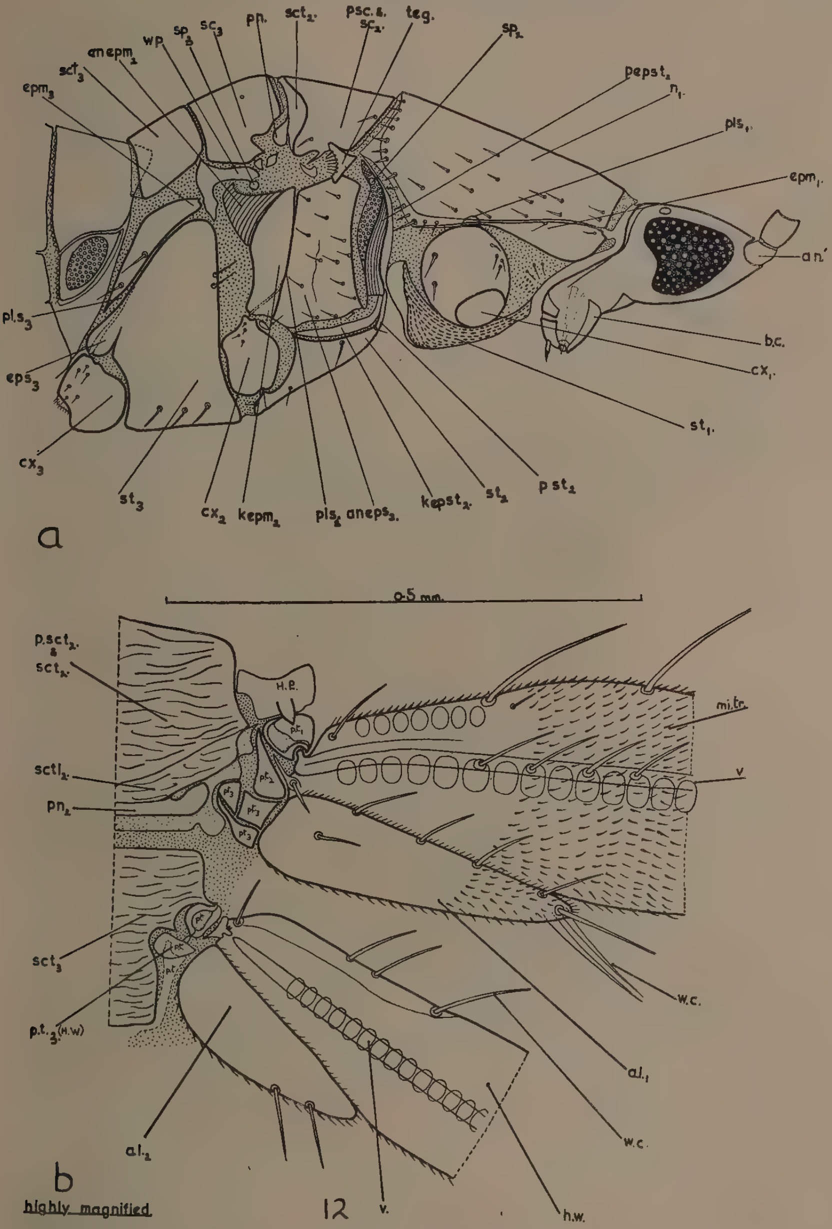
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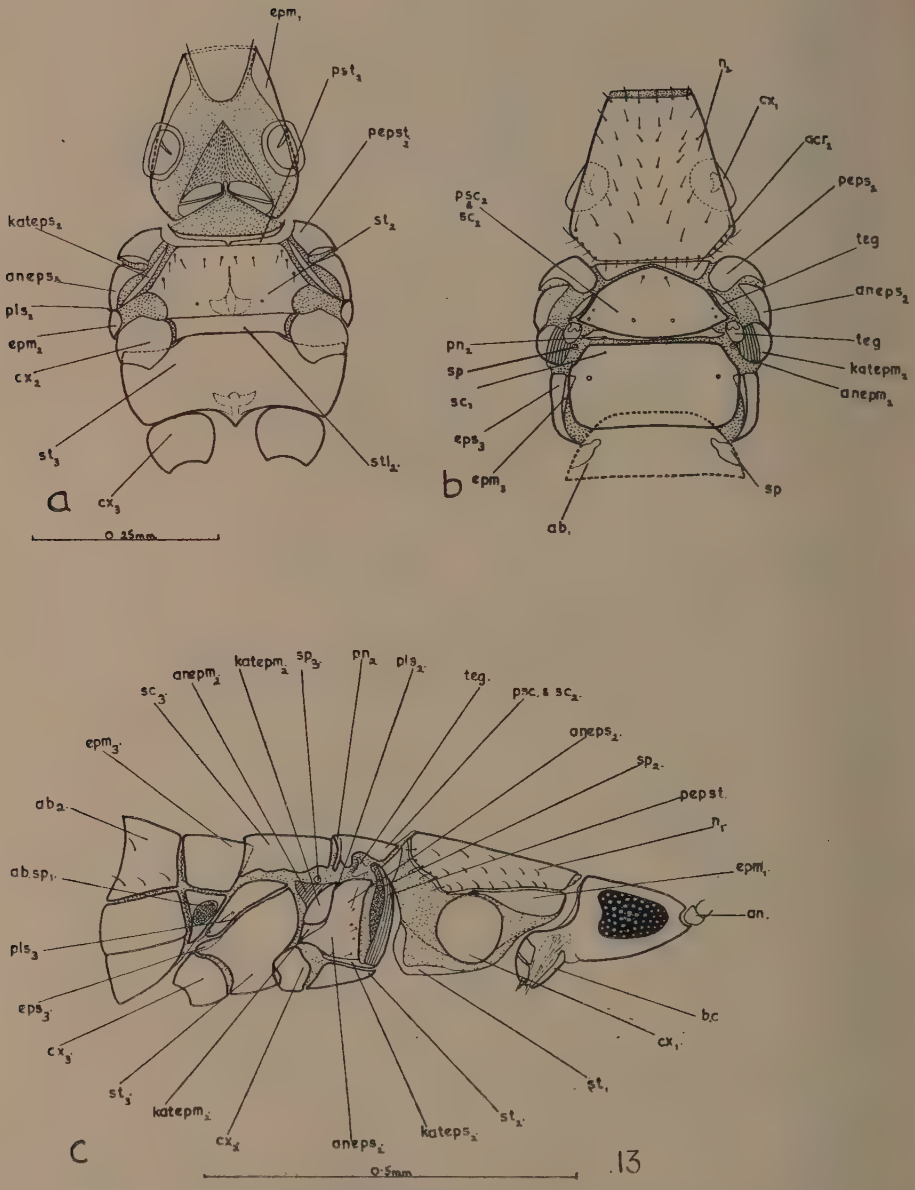
FIG. 12.—*C. hamatus.* (*a*) Lateral view of the female thorax. *an^1*, antenna; *anepm*, anepimeron; *aneps*, anepisternum; *bc*, buccal cone; *cx*, coxa; *epm*, epimeron; *eps*, episternum; *kepst*, katepisternum; *kepm*, katepimeron; *pls*, pleural suture; *pepst*, pre-episternum; n_1, pronotum; *pn*, postnotum; *psc* and *sc*, prescutum and scutum; *pst*, presternum; *sct*, scutellum; *sc*, scutum; *st*, sternum; *sp*, spiracle; *teg*, tegula; *wp*, wing process. (*b*) Wing bases, high magnification. *al*, anal lobe; *hp*, humeral plate; *hw*, hind wing; *mi.tr*, microtrichia; pn_2, postnotum; $psct_2$, prescutum; sct_2, scutum; *pt*, pteralia; $sctl_2$, scutellum; *v*, vein; *wc*, wing coupling. Scale line refers to 12*a*.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13

FIG. 13.—*C. hamatus*. (*a*) Ventral view of male thorax. Lettering as in fig. 11(*a*). (*b*) Dorsal view of male thorax. Lettering as in fig. 11(*b*). (*c*) Lateral view of male thorax. Lettering as in fig. 12(*a*).

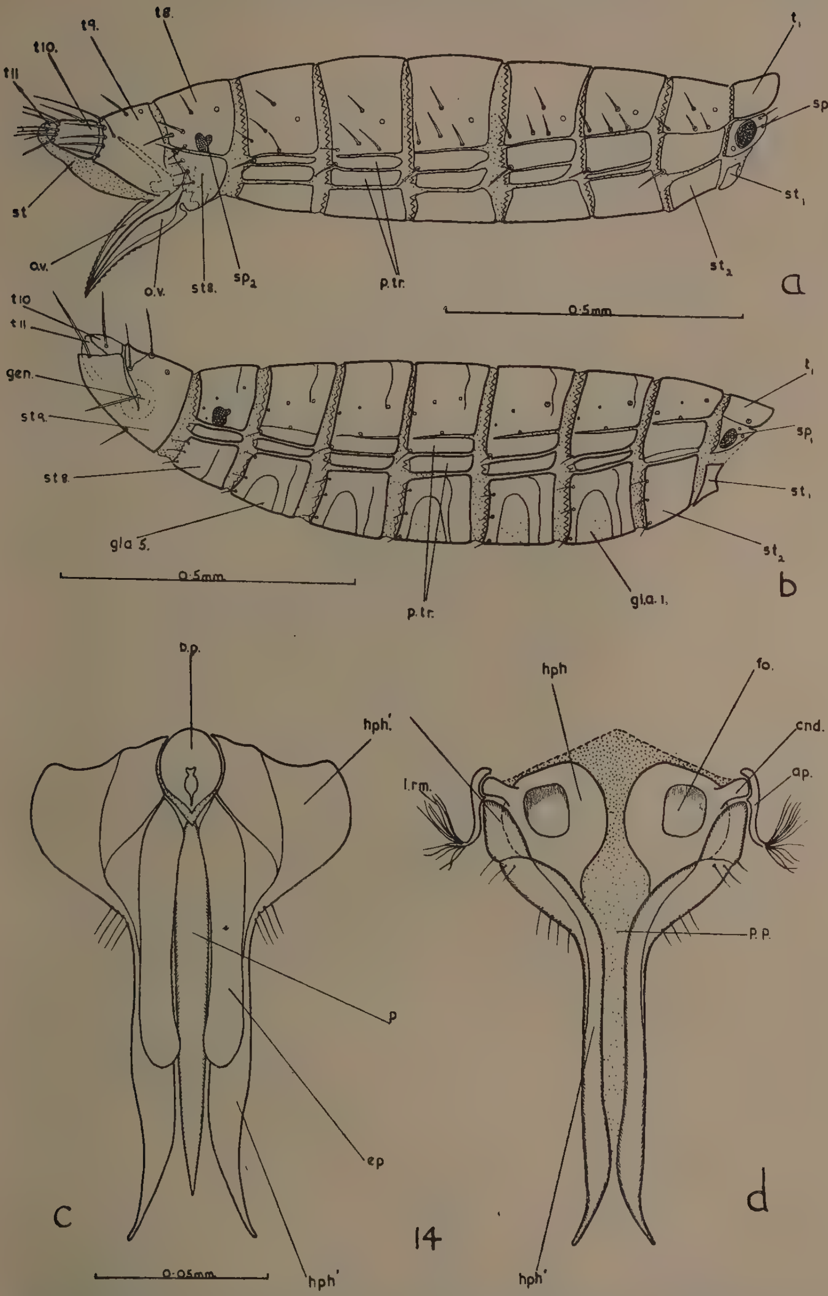
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FIG. 14.—*C. hamatus.* (*a*) Lateral view of female abdomen. *ov*, ovipositor; *p.tr*, pleurotergites; *sp*, spiracle; *st*, sternum; *t*, tergum. (*b*) Lateral view of male abdomen. *gen*, genitalia; *gla*, glandular areas. Other lettering as in fig. 14(*a*). (*c*) Dorsal view of male genitalia. *bp*, basal piece; *ep*, epiphallus; *hph*, valves of hypophallus; *p*, penis. (*d*) Ventral view of male genitalia. *ap*, apodeme; *cnd*, condyle of periandrium; *fo*, foramen; *hph*, hypophallus; *lrm*, lateral retractor muscle; *pp*, position of penis.

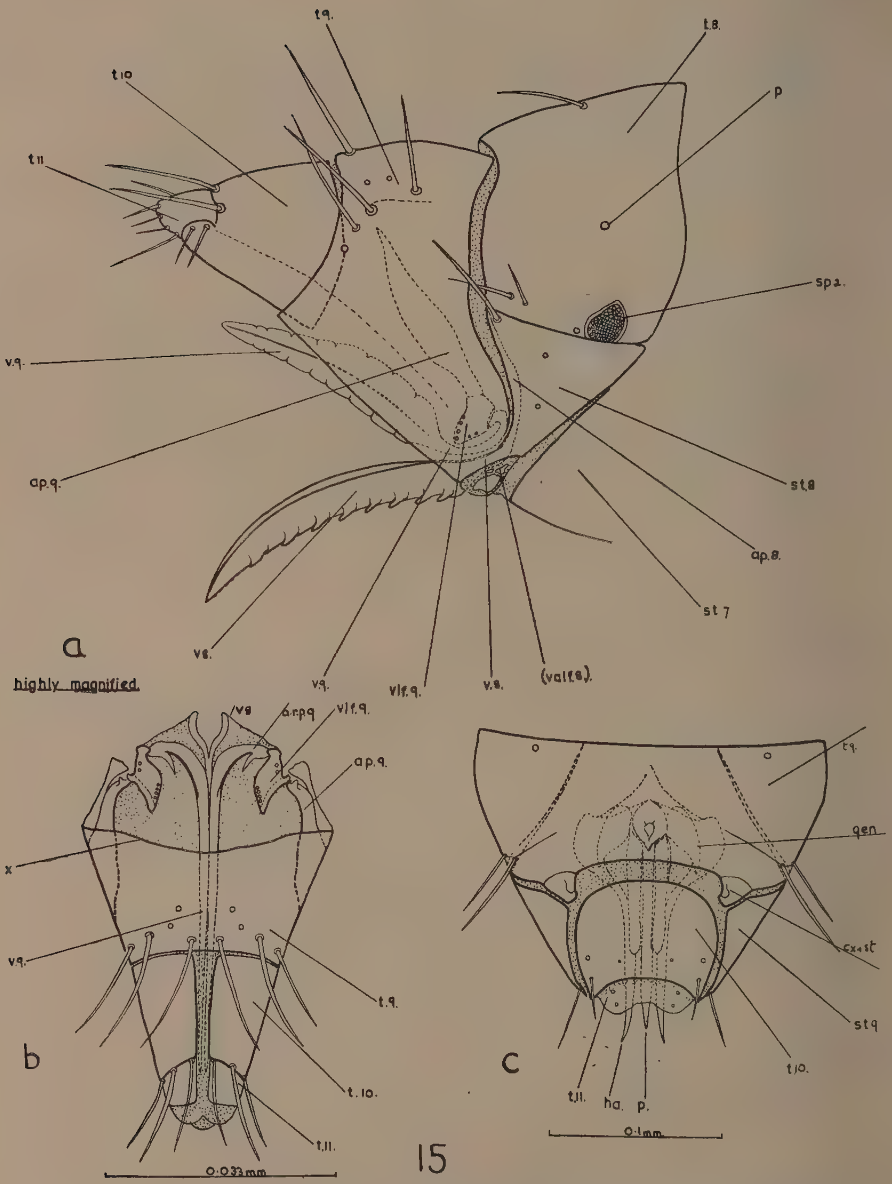
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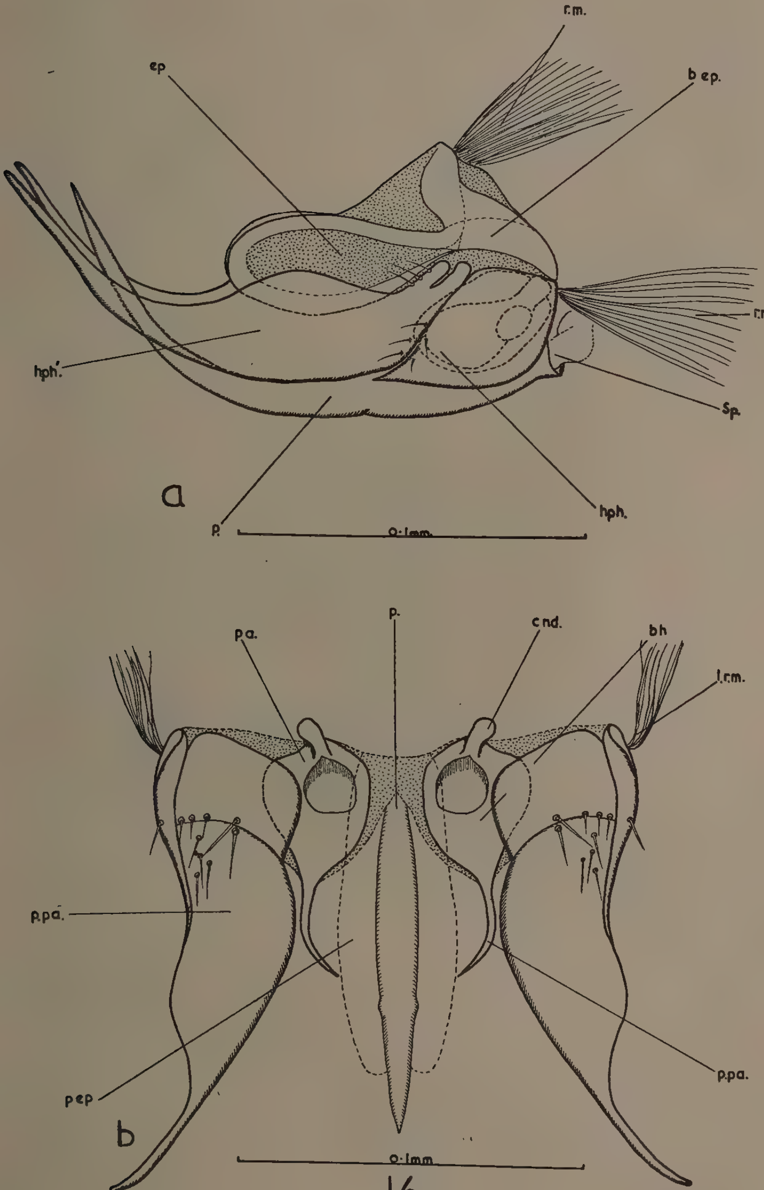
Fig. 15.—*C. hamatus.* (*a*) Lateral view of distal end of female abdomen. *ap*, apodeme; *p*, pore; sp_2, spiracle; *st*, sternum; *t*, tergum; *v*, ovipositor valve; *valf*.8, first valvifer; *vlf*.9, second valvifer. (*b*) Dorsal view distal end of female abdomen. *ar.p*, articulatory process. Other lettering as in fig. 15(*a*). (*c*) Dorsal view distal end of male abdomen. Lettering as in fig. 8.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p.pa.
pep
b
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16

FIG. 16.—*C. hamatus.* (*a*) Lateral view of the complete male genitalia. *bep*, base of epiphallus; *ep*, epiphallus; *hph*[1], ventral valve of hypophallus; *p*, penis; *rm*, retractor muscle; *sp*, spermathecal pouch. (*b*) Dorsal view of the dissected male genitalia. *bh*, base of ventral valve of hypophallus; *cnd*, condyle; *lrm*, lateral retractor muscle; *p*, penis; *pa*, periandrium; *pep*, position of epiphallus; *p.pa*, process of periandrium.

Vol. 105. Part 11. Pp. 189–239. 24 figs., 1 map. 15th July, 1954

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   Prof. G. C. Varley, appointed 1952.
   Dr. E. B. Ford, F.R.S., appointed 1949.
2. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten, O.B.E. (nominated by Committee for the Protection of British Insects).
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. H. M. Edelsten, O.B.E., appointed 1944.
4. **New Forest Association.**
   Mr. C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
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8. **Yorkshire Naturalists' Trust, Ltd.**
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9. **The Biological Council.**
   Dr. N. E. Hickin, appointed 1952.
10. **The Parliamentary and Scientific Committee.**
    Dr. N. E. Hickin, appointed 1953.

A MONOGRAPH OF THE CONCHASPIDIDAE GREEN (HEMIPTERA: COCCOIDEA).

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Manuscript received 7th August, 1953.

(Read 4th November, 1953.)

With 25 Text-figures.

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I. Description of the Family Conchaspididae Green.

1896, Conchaspinae Green, *The Coccidae of Ceylon*, **1** : 17, 19. (The name Conchaspinae introduced for the first time and accompanied by a short diagnosis. *Conchaspis* Cockerell, the only included genus, becomes automatically the type genus.)

1899, Chonchaspidinae Green (*sic*), Green, *J. Bombay nat. Hist. Soc.* **13** : 66. (An inadmissible emendation of the name Conchaspinae.)

1903, Conchaspinae Green, Newstead, *A Monograph of the Coccidae of the British Isles*, **2** : 1. (Green's diagnosis (1896) repeated and one additional character given.)

1903, Conchaspinae Green, Fernald, *A Catalogue of the Coccidae of the World*, 38. (Gives a complete list of bibliographical references to the family.)

1918, Conchaspinae Green, Brain, *Bull. ent. Res.* **9** : 113. (Green's original diagnosis repeated with the addition of one character.)

1921, Conchaspinae Green, MacGillivray, *The Coccidae*, 212. (An exhaustive list of distinguishing features given, some of which are totally erroneous; also general remarks based on known species and accompanied by a key to the species of the type genus *Conchaspis*.)

1932, Conchaspididae Green, Brues and Melander, *Bull. Mus. comp. Zool.* **73** : 131. (Apparently the first to give the group family status. Brief distinguishing features given.)

1937, Conchaspidae Green, Ferris, *Atlas of the Scale Insects of North America*, Series 1 : 6. (Brief general remarks on the family : here, as in the two subsequent references, the family name is incorrectly spelt.)

1942, Conchaspidae Green, Balachowsky, *Ann. Ecole nat. Agric., Grignon*, **3** : 37. (Differentiates the family from others.)

1948, Conchaspidae Green, Balachowsky, *Les Cochenilles de France, d'Europe, du Nord de l'Afrique et du Bassin Méditerranéen*, **4** : 8. (A short discussion on the status of the family given.)

Coccoidea, distinguished by the absence of certain structures which are found in other families; thus, without abdominal spiracles (Margarodidae, Ortheziidae); without branchiae or branchial plates (Lacciferidae); without ostioles or cerarii (Pseudococcidae); without ventral cicatrices; without anal cleft or an operculum covering the inner end of this cleft (Coccidae); without anal plates; without ducts having an inner laterally placed filament; without 8-shaped pores (Asterolecaniidae); without a pygidium formed by the complete fusion of the fifth to eleventh abdominal segments (Diaspididae); without setigerous anal ring.

With well-developed antennae and legs in all stages, the legs with the tibia and tarsus always fused; with eyes developed in all immature stages; with dorsal " ocellar spots " in the immature stages of both sexes.

The adult female with well-developed dorsal " ocellar spots " and one pair of dermal invaginations or pits on the venter of the metathorax, a little caudad from the insertion of the third pair of legs. Also, in the adult female of at least one species of the type genus, another pair of similar invaginations on the venter of the mesothorax, a little caudad from the insertion of the second pair of legs. With dorsal tubular pores with slit-like openings, or with peculiar ventral multilocular pores, or with both types of pores. With anus not invaginated, opening at the posterior apex of the abdomen on the ninth or tenth segment and accompanied neither by pores nor by setae. With seventh to eleventh abdominal segments fused into a pseudopygidium. With spiracles not of the Beesonid type.

The immature stages, except the first, of both sexes, as well as the adult female, protected by a scale covering formed by secretion from the underlying insects, as in the Diaspididae, but in which no exuviae are incorporated.

The adult male with two pairs of ocelli, one ventral and one dorsal; with antennae 6–7-segmented with the terminal segment not elongated; with well-developed wings; with halteres bearing only one hair; with tibia and tarsus always fused; with a long, slender stylus; without a definite neck between the head and the thorax.

The first stage larva with antennae 6-segmented, the terminal segment not being of the Diaspidid type; with submarginal eyes; with dorsal " ocellar spots " not as developed as in the adult female; with tibio-tarsal suture wanting in all legs; with large tubular dorsal pores with slit-like openings sometimes on the margin of the most anterior abdominal segments; with posterior segments of the abdomen fused into a pseudopygidium; with anal opening non-cellular and not setigerous, and situated at the apex of the pseudopygidium.

Type genus : *Conchaspis* Cockerell (1893).

II. THE SYSTEMATIC POSITION OF THE CONCHASPIDIDAE.

When Cockerell described the genus *Conchapsis* under the heading " Aberrant genus " (1893, *Bull. bot. Dep. Jamaica*, **40** : 9), he cited the opinion of L. O. Howard that this genus did " not seem to belong to the Diaspinae " and that " the characters of the last segment as well as the presence of antennae and legs would place it in the Coccinae, and possibly in the Acanthococcini . . . " and that " . . . the anal characters would remove it from the Lecaniinae . . . "

In 1896 Cockerell (*Bull. Illinois St. Lab. nat. Hist.* **4** : 323) placed the genus *Conchaspis* among the " Coccinae " in which he included the now-recognised Dactylopiidae, Pseudococcidae and Kermidae.

The same year Green (1896, *Coccidae of Ceylon*, **1** : 20.) pointed out that the Conchaspididae (= Conchaspinae) had some affinity with the " Coccinae." Later, in 1922, the same author (1922, *Coccidae of Ceylon*, **5** : 459), on the basis of a better knowledge of the classification of the Coccoidea, synonymised his " Coccinae " with the " Dactylopiinae" which then comprised what are now the Dactylopiidae and the Pseudococcidae.

In 1899 Cockerell (*Canad. Ent.* **31** : 275) placed the Conchaspididae (= Conchaspinae) between the Margarodidae (= Margarodinae) and the " Coccinae '. which included the present Asterolecaniidae, Kermidae, Pseudococcidae, etc.

In 1903 Newstead (*Monograph of the Coccidae of the British Isles*, **2** : 1) stated that the Conchaspididae (= Conchaspinae) were more closely related to the Diaspididae (= Diaspinae) than to any other division of the Coccoidea (= Coccidae).

Fernald (1903, *Catalogue of the Coccidae of the World:* 38) listed the Conchaspididae (= Conchaspinae) between the Phenacoleachiidae and the " Dactylopiinae," the latter being composed of a mixture of the now-recognised Dactylopiidae, Kermidae and Asterolecaniidae.

MacGillivray (1921, *The Coccidae:* 212) placed the family in a position intermediate between the Cylindrococcinae (in which he included the Phoenicococcinae of the family Diaspididae) and the Diaspididae (= Diaspinae).

In 1937 Green, in his *Annotated List of the Coccidae of Ceylon, with Emendations and Additions to date* (1937, *Spolia zeylan.* **20** : 313) listed the Conchaspididae (= Conchaspinae) between what he called the " Lecaniinae" (the present Coccidae) among which he included the genus *Aclerda* which is the type of the family Aclerdidae, and the Diaspididae (= Diaspidinae).

Ferris (1937, *Atlas of the Scale Insects of North America, Series* **1** : 6.) placed the Conchaspididae (= Conchaspidae) between the Coccidae and the Diaspididae.

Balachowsky, in his *Essai sur la classification des Cochenilles* (1942, *Ann. Ecole nat. Agric. Grignon*, (3) **3** : 37) and in his work on *Les Cochenilles de France, d'Europe, du Nord de l'Afrique et du Bassin Méditerranéen* (1948, **4** : 12, 17, 19), divided the Coccoidea into three large groups and relegated the Conchaspididae (= Conchaspidae) in the " Lecanoidae " which comprise all the families of the Coccoidea except the Margarodidae, Ortheziidae, Diaspididae and " Phoenicococcidae."

Several of the above-quoted authors have based their conclusions concerning the systematic position of the Conchaspididae on the characters of the mentum. Balachowsky has, in addition, made use of the characters found in the adult male and has also laid stress on the presence or absence of certain types of pores in the female.

All the postembryonic stages of both the female and male of some Conchaspidids have been available to the author during the course of this study. These immature stages have helped him to arrive at the following conclusion which he thinks reasonable.

The segmentation of the mentum, on which some authors have laid much emphasis in the classification of the families of the Coccoidea, should not, in the writer's opinion, be taken as diagnostic since this organ may be either monomerous or dimerous in the same family. Moreover, the mentum is somewhat retractile and when viewed at a certain angle appears subcircular or oval, as is generally the case with the Diaspidids and with some species of Conchaspidids.

The presence of tubular pores in the Conchaspididae—pores which are not unlike those found in the Diaspididae—is a point which should be borne in mind when considering the systematic position of the family. As far as the author is aware, tubular pores of the type found in the Conchaspididae are not identical with the types found in any other family (a description of these pores is given below). They seem nevertheless to be more closely related to those found in the Diaspididae than to those which occur in other families, and they are usually grouped into well-defined clusters, as in the Diaspididae.

The multilocular pores of the type found in certain members of the Conchaspididae have apparently no counterpart in any of the other families of the Coccoidea, being quite different from those which occur in the Margarodidae, Coccidae, Diaspididae, Pseudococcidae, etc.

The anus of the female and immature stages of the Conchaspididae is not protected by and does not occur between or under plate-like structures as in the Coccidae, Aclerdidae, some Asterolecaniidae, etc. It is also not furnished with hairs (cf. the Pseudococcidae, Kermidae, Coccidae, Ortheziidae, etc.) and is not associated with pores.

The male insect which, as pointed out by Balachowsky, is of value in the classification of the superfamily, has characters which are more akin to the "Diaspidoid" side than to the "Lecanoid," both terms having the meaning given to them by Balachowsky (*loc. cit.*). The only point on which the males of those Conchaspidids which were available to the author does not fully agree with the description of the "diaspidoid" male, as given by Balachowsky (*loc. cit.*), is in the *complete* fusion of the head and the thorax and the consequent total absence of a "neck." It should be emphasised that the Conchaspidid male does not conform with the description of the "lecanoid" type on the same character. In the Conchaspidid male no definite "neck" is present, the head is only partly fused to the thorax medially. On this character alone, this male appears therefore to be intermediate between the "diaspidoid" and the "lecanoid" types. Other characters have therefore to be examined in order to reach a conclusion as to whether the Conchaspidid male is more closely related to the "diaspidoid" than to the "lecanoid" type. In the Conchaspidid male, the halteres bear only one hair and the stylus is elongate. These characters are typical of the "diaspidoid" type. Also, other characters, for example, those found in the sclerotisation of the thorax—though perhaps having minor value—tend to show that the Conchaspidid male has more affinities with the "Diaspidoids" than with the "Lecanoids." It differs, however, from the "diaspidoid" male by the constitution of the antennae and of the legs. In conclusion, it seems that we are here dealing with a third type of male—the "Conchaspidoid" type (to employ the same terminology as that used by Balachowsky)—which is more closely related to the "diaspidoid" than to the "lecanoid" type.

The Conchaspididae seem therefore more closely related to the Diaspididae than to the other families of the Coccoidea.

III. The Genera of the conchaspididae

Four genera have hitherto been assigned to this family ; they are :

1. *Archaspis* Bodenheimer (type : *A. ephedrae* Bodenheimer), described from Iraq (1943, *Bull Direct. Agric Minist. Econ. Iraq*, **28** : 25).
2. *Scutare* Brittin (type : *S. fimbriata* Brittin), described from New Zealand (1914, *Trans. N. Z. Inst.* **47** : 158).
3. *Fagisuga* Lindinger (type : *F. triloba* Lindinger), described from Chili (1909, *Z. wiss. Insekt. Biol.* **5** : 107).
4. *Conchaspis* Cockerell (type : *C. angraeci* Cockerell), described from Jamaica (1893, *Bull. bot. Dep. Jamaica* **40** : 9).

1. *Archaspis* Bodenheimer.

The author agrees with Balachowsky's views (1948, *loc. cit.*) that the genus *Archaspis* Bodenheimer has been based on either an aberrant form of a Diaspidid, or, much more probably, on the first stage of some species of the same family. *Archaspis* should therefore be removed from the Conchaspididae and transferred to the Diaspididae.

As a result of this new assignment, it follows that Bodenheimer's theory on the phylogeny of the Diaspididae (1944, *Proc. R. ent. Soc. Lond.* (B), **13** : 4–5) is not tenable since it was entirely based on the genus *Archaspis* as a member of the Conchaspididae.

2. *Scutare* Brittin.

The writer has been informed by the Assistant Director of the Cawthron Institute, New Zealand, that the type slide of *Scutare fimbriata* Brittin (the type species of *Scutare*) had apparently not been preserved by this author. Material of what Brittin himself identified as " *Rhizococcus fimbriatus* Brittin " was, however, kindly supplied and has been found to agree very closely with the description and figures of *Scutare fimbriata*. It seems therefore evident that Brittin himself was of the opinion that his *Scutare fimbriata* had originally been generically misplaced and that the species should have rather been assigned to the genus *Rhizococcus* Signoret. After carefully studying the above-mentioned material, the author has also reached the conclusion that *Scutare* Brittin is definitely a synonym of *Rhizococcus* Signoret (*syn. nov.*). The genus *Scutare* should therefore be removed from the Conchaspididae and referred to the Kermidae in which *Rhizococcus* fits well.

3. *Fagisuga* Lindinger.

The author concurs with Balachowsky's opinion (1948, *loc. cit.* : 17) that *Fagisuga* Lindinger, of which specimens of the type species (*triloba* Lindinger) kindly made available to him by Prof. G. F. Ferris have been studied, should be referred to the Phoenicococcinae of the Diaspididae.

4. *Conchaspis* Cockerell.

The genus *Conchaspis* is the only group which should remain in the family. A detailed account of this genus is therefore given in the subsequent paragraphs.

IV. THE GENUS *Conchaspis* COCKERELL.

LITERATURE.

1893, *Conchaspis* Cockerell, *Bull. bot. Dep. Jamaica*, **40** : 9, February (published March). (The name *Conchaspis* introduced for the first time with a short diagnosis ; *C. angraeci* indicated as the only included species, without description ; monotypical genus.)

1893, *Conchaspis*, Cockerell, Cockerell, *J. Inst. Jamaica*, **1** : 256, April (published May). (The names *Conchaspis* and *C. angraeci* listed without description but accompanied by a sketch of the female scale of the species.)

1893, *Conchaspis* Cockerell, Cockerell, *Gdnrs.' Chron.* (3), **13** : 548 (published May 6th). (The name *Conchaspis* again introduced as a " n. g." ; no additional description of it given ; *angraeci* briefly described as only included species.)

1893, *Pseudinglisia* Newstead, *Ent. mon. Mag.* **29** : 153. (Genotype : *Pseudinglisia rodrigueziae* Newstead ; a short description of this genus given.)

1895, *Conchaspis* Cockerell, Cockerell, *Bull. bot. Dep. Jamaica* (N.S.) **2** : 101. (Brief description of the genus ; indication that *Pseudinglisia* Newstead may be a synonym of it.)

1896, *Conchaspis* Cockerell, Cockerell, *Tech. Bull. U.S. Dep. Agric.* **4** : 36. (List of all bibliographical references to the genus.)

1896, *Conchaspis* Cockerell, Green, *The Coccidae of Ceylon*, **1** : 19. (Formal recognition of the genus accompanied by a short description ; erection of subfamily Conchaspinae.)

1899, *Chonchaspis* Cockerell (*sic*), Green, *J. Bombay nat. Hist. Soc.* **13** : 66. (An inadmissible emendation of the name *Conchaspis.*)

1903, *Conchaspis* Cockerell, Fernald, *A Catalogue of the Coccidae of the World* : 38. (List of all bibliographical references to the genus and to the species known at that date; *Pseudinglisia* Newstead listed as a synonym of the genus.)

1903, *Conchaspis* Cockerell, Newstead, *A Monograph of the Coccidae of the British Isles*, **2** : 1. (Additional features of genus given ; *Pseudinglisia* Newstead formally synonymised.)

1921, *Conchaspis* Cockerell, Macgillivray, *The Coccidae* : 215. (Separates the genus from the other genera at that time included in the family ; key to known species of *Conchaspis* given.)

Type of the genus : *Conchaspis angraeci* Cockerell (1893).

Distinguishing characters.—The characters given for the family will be adequate for the recognition of the genus. More detailed characters, and discussion thereon, are given in the following paragraphs.

1. Morphology of the adult female.

Body Form and Derm.

The body form does not vary much among the members of the genus. It resembles somewhat that of certain members of the Diaspididae in having a well-developed prosoma, which at times is markedly swollen, and a postsoma in which the most posterior segments are partly fused into a kind of pygidium, or " pseudopygidium ," as it will be referred to in this study.

The derm may be membranous or slightly sclerotised. It nearly always exhibits a certain stippling which is due to the occurrence of sclerotised dots of variable dimensions and of irregular shapes and which vary considerably between the different species. The derm may thus be said to be " shagreen-like," " coarsely stippled," or " finely stippled," as the case may be. The degree of stippling is a useful character in the identification of some species. There is apparently no difference in the stippling of both the dorsal and ventral surfaces.

The posterior segments of the abdomen nearly always show a common plan of sclerotisation. This sclerotisation takes the form of well-defined dorsal and ventral areas on each segment and these areas are always interrupted medially, especially on the venter. The name of " sclerotized plates " has been given to these areas by certain authors.

The Prosoma.

The prosoma, which is essentially composed of the cephalic and of the three thoracic segments, is usually swollen. The divisions between the segments of the prosoma are sometimes quite apparent in the species in which the derm is either shagreen-like or coarsely stippled.

The cephalic segments.—The head bears the mouth-parts, the ventral antennae and a pair of peculiar dorsal structures which have been given the name of " eye spots " but which, in the author's opinion, should rather be known as the " dorsal ocellar spots." In some species, a definite segmentation exists between the head and the first thoracic segment ; in others, especially in the species in which the derm is finely stippled, this segmentation is not apparent.

The mouth-parts are well-developed ; the mentum or beak is two-segmented and bears a few setae near its apical end.

The antennae, which are ventral, are moderately developed and consist of from 2 to 5 segments of which those of the extremity bear conspicuous, hyaline, broad, thick and bluntly-pointed sensory setae, and also a few ordinary setae. The terminal segment, though sometimes elongate, is not the longest ; on the contrary, it is sometimes the shortest. The antennae are either marginal or submarginal in position and the number of their segments is constant for each species. In all other characters, the antennae do not afford any reliable basis for specific determination.

On the dorsal surface of the head, somewhat centrally, lie a pair of characteristic structures which are the " dorsal ocellar spots." These structures have been known by most authors as the " eye-spots." They apparently have nothing to do with the true eyes. It has been observed that, in the first-stage larvae and all the other immature stages that have been available to the author, the true eyes are present marginally or submarginally and that in these same stages the " spots " also occur. It is therefore considered that these structures represent ocelli similar to those which are found in the adult males of the genus, though much larger. The appellation " dorsal ocellar spots " seems therefore more appropriate for them. In some species, these " ocellar spots " are very conspicuous, being circumscribed by a ring of chitin within which a well-sclerotised disc occurs centrally. In other species, the external ring of chitin may be broad and open either anteriorly or posteriorly. In others still, these spots, being membranous, are somewhat difficult to observe unless the specimens are fairly strongly stained. These " dorsal ocellar spots " have been found to be of specific importance and are sometimes very helpful in the separation of related species.

The cephalic setae.—In all the species so far examined, the setae that occur on the ventral surface of the head are usually longer and stouter than those on the dorsal surface. Usually, three pairs of long ventral setae occur on the frontal area and a smaller pair near the base of each antenna. The dorsal setae are very much shorter and vary in size and length with the different species.

The thoracic segments.—The segmentation between the thoracic segments is well-marked especially in those species where the derm is shagreen-like or coarsely stippled.

The prothorax bears marginally or submarginally on the dorsal surface a conspicuous tubercle, which is referred to in this study as the "prothoracic tubercle." The cuticle of this tubercle is always smooth, even in species in which the derm is coarsely stippled.

The legs are well-developed and the trochanter, in most species, is partly fused with the femur. There is also no articulation between the tibia and the tarsus, these two pieces being thoroughly fused together in the three pairs of legs so as to form the tibio-tarsus. The claw is well-developed and generally bears on its plantar surface a minute tooth. In a few species, this tooth is not apparent and it may be taken that it does not exist. No significance has been given to this character in the present study. The legs do not furnish any reliable character for the separation of the species.

Tubular pores (of which an account is given below) may or may not be present on the basal angles of the metathorax dorso-laterally.

Multilocular pores, which are described below, are generally absent on the prosoma of nearly all the species of the genus, except, however, in *C. insolitus* sp. n., in which they occur in small numbers submarginally.

As in all other members of the Coccoidea, two pairs of spiracles occur on the thoracic segments. They are situated on slightly raised tubercles which occur latero-ventrally and fairly close to the margin of the mesothorax and of the metathorax. The openings of the spiracles are usually accompanied by a few pores having five loculi.

The dermal invaginations of the thorax.—There occurs on the ventral side of the metathorax of adult females, a little caudad from the coxae of the third legs, a dermal "invagination" or "pit" or "pocket" which is usually well-sclerotised. These metathoracic invaginations are present in all the species of the genus, but are of no value as a means of distinguishing the species. In one of the species examined (*C. madagascariensis* sp. n.) a second pair of invaginations is present in a similar position on the mesothorax. The author considers that the occurrence of this extra pair of invaginations in *C. madagascariensis* does not warrant, at this juncture, the creation of a new genus.

These metathoracic invaginations have been assumed by some authors to occur on the first abdominal segment. This is not so; they definitely form part of the metathorax, although sometimes they occur on the fold separating this segment from the first abdominal segment. Most authors have considered this metathoracic (or, first abdominal, as they call it) invagination to be a non-functional spiracle, but this is most unlikely, for the invaginations are ventral, and, as already stated, do not occur on the first abdominal segment. The author's contention is strengthened by the presence of similar structures on the mesothorax of *C. madagascariensis* in a position similar to those on the metathorax. Typically, the mesothorax of insects bears only one pair of functional spiracles, one on each side. As far as the author is aware, two pairs of spiracles, whether functional or not, never occur on the same segment in the Coccoidea and in most of the other insects except, however, the Diplura, which is a group of very specialised forms. It follows therefore that structures which occur on the mesothorax in addition to the functional spiracles cannot be considered as " non-functional spiracles " and the terms " dermal invaginations " or " dermal pits " are appropriate names for them. It follows, by analogy, that the metathoracic structures which are found in a similar position and which have a similar morphology as those of the mesothorax should also be considered as " dermal invaginations " or " dermal pits." These invaginations or pits are absent, i.e., not developed, in all stages preceding that of the adult female. They do not occur in any stage of the male insect.

The Postsoma.

The postsoma is composed of the abdominal segments only. In the abdomen of the Conchaspididae, the six proximal segments are free and the distal segments are partially fused into a pygidium, as in the Diaspididae. To differentiate between the pygidium of the Conchaspididae in which no conspicuous lobes occur and that of the Diaspididae in which lobes and other structures are usually found, it is proposed to adopt the term " pseudopygidium " for this partially fused piece.

The pseudopygidium of Conchaspidids is composed of the seventh to the eleventh segments. The seventh and eighth segments can be easily distinguished by the position of the marginal setae, and to a lesser degree medially. The ninth to the eleventh segments are obscure and are apparently very poorly developed.

The anus is situated at the apical extremity of the pseudopygidium and presumably opens on the ninth or tenth segment, in a slit in the pleurae of these segments. The position of the anus in the Conchaspididae had long been uncertain for it is concealed by the structures between which it occurs. The anus is accompanied neither by pores nor by setae and there are no true anal plates as in the Coccidae. It is therefore of no taxonomic utility for the separation of species.

The vulva lies apparently on the sixth or the seventh abdominal segment ventrally and is well-developed in all the species.

Pores and ducts.—Two types of pores and ducts are present in the members of this genus : (i) a multilocular stellate pore, and (ii) a tubular pore with elliptical to slit-like opening. These pores and ducts are of great help in the identification of the species.

(i) *The multilocular pore.*—When present, these pores always occur on the ventral surface of the body. They are borne on slightly sclerotised discs and consist essentially of a thick outer ring which is crenulate so as to fit a first series of clear, roundish to oval openings of which there are usually 10 to 13 in number. Within this ring of openings, there is a delicate ring-like partition within which occurs another series of very small openings, usually 10 to 13 in number. These openings are in turn separated from the central core of the pore by another delicate ring-like partition. It has been found difficult to determine the nature of the central part or core of these multilocular pores.

Pores of this type generally occur marginally or submarginally, singly or in small groups on the free segments of the abdomen. In only one species, *C. insolitus* sp. n., they are also present on the head and the thorax submarginally. In a few other species, there are, in addition to the marginal or submarginal groups on the abdominal segments, a few pores in a submedian position and in a position intermediate between the submedian and the submarginal groups.

The multilocular pores vary much in size from one species to another, though the same number of loculi occurs in them.

(ii) *The tubular ducts.*—Pores having tubular ducts, which are apparently formed by the invagination of the body wall, are found only on the dorsal surface of the body. When present, they occur generally in a submarginal and marginal position on the basal angle of the metathorax and of the free abdominal segments. Two types are sometimes found : a large and a small, both types having the same structure. The openings of these ducts are more slit-like than oval or elliptical and are sometimes well-sclerotised. The ducts themselves are also somewhat sclerotised and their inner extremity is truncate and well-sclerotised and seems to bear minute pore-like areas marginally. It is presumed that wax may be secreted by these pore-like spots. No histological study of these tubular pores has yet been carried out but it has been found that their inner termination is neither cup-shaped nor dome-shaped and without side filament, as in the Coccidae, Pseudococcidae and other families, nor is it similar to that of the ducts found in the Diaspididae.

Abdominal tubercles.—Structures resembling little tubercles with either rounded, smooth or finely-serrated or digitate apices occur on the venter of certain abdominal segments submarginally in a few members of the genus. They are the "tuberculos mamiliformes" of Lepage, which should rather be called the "abdominal tubercles." No duct or pore is associated with these tubercles.

2. Morphology of the immature female stages.

(i) *The First Stage Female* (fig. 1).

Species examined : *C. angraeci* Cockerell, *euphorbiae* Brain, *diplothemii* Lepage and Giannotti, *socialis* Green, *vaughani* sp. n., *vayssierei* sp. n.

The first stage female, which is not protected by a scale, has a somewhat oval shape. The derm may be membranous and may also be finely or coarsely stippled. The antennae are 6-segmented and the sixth segment, though elongate, is not the longest and does not show the annular striations found in certain members of the Diaspididae ; the fifth segment usually bears a thick sensory hair. The eyes are always present marginally or submarginally. The dorsal ocellar spots are also present but are less pronounced than those found in the adult female of the same species. The mouth-parts are strongly developed and the mentum is dimerous. The legs are well-developed ; the tibio-tarsal suture is wanting in the three pairs while the trochantero-femoral suture is fairly conspicuous. The claw is well-developed and bears a denticle on its plantar surface (at least in the species of which this stage was available) ;

the ungual and tarsal digitules are long and hair-like, those of the claw have knobbed extremities. The two pairs of spiracles are normal and are usually accompanied by very few (1–2) pores with five loculi. The ventral metathoracic dermal invaginations are always wanting. The abdominal segmentation is distinct both dorsally and ventrally; the pseudopygidium is composed of the seventh to eleventh segments and the other segments are free. The apical extremity of the pseudopygidium is similar to that of the adult female but its sclerotisation is less pronounced. The anus is neither accompanied by pores nor by setae and is also neither protected nor bordered by sclerotised plates; it opens at the apex of the pseudopygidium. A short and slightly sclerotised anal tube may or may not be present. The dorsal tubular pores may be present or absent, when present they occur on the lateral margin of the anterior

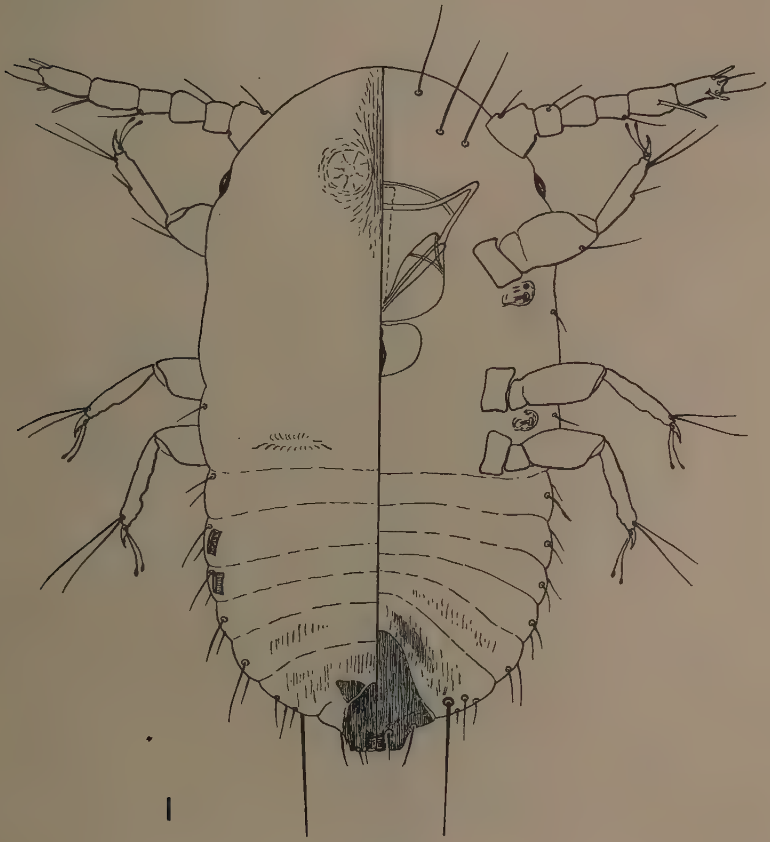

Fig. 1.—*Conchaspis vayssierei* Mamet, sp. n. First stage larva.

abdominal segments. Other types of pores are always absent. The body setae are very conspicuous especially on the margin of the abdominal segments and on the ventral surface of the frons. A long and stout seta is in addition present on the sixth abdominal segment submarginally.

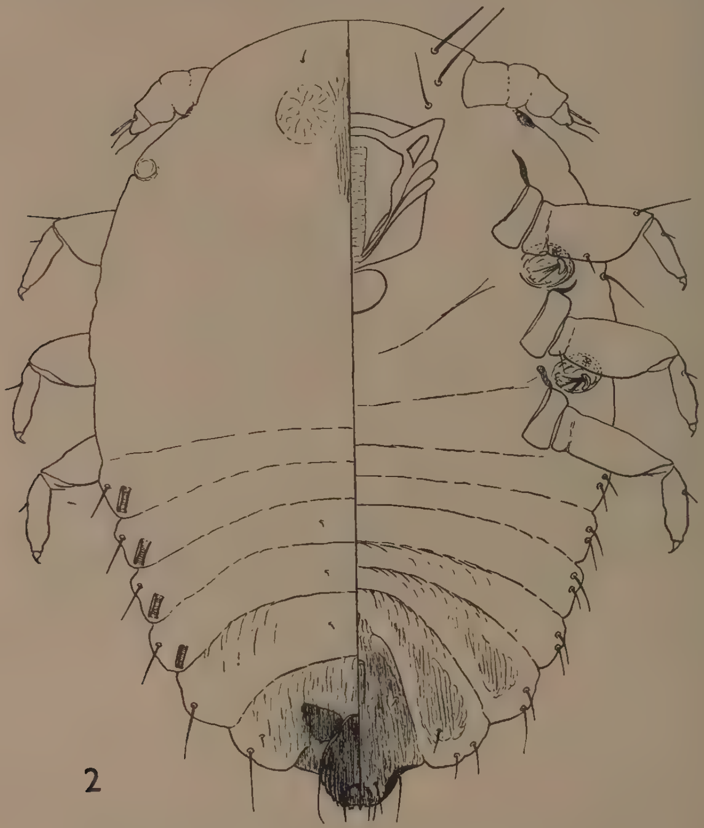

FIG. 2.—*Conchaspis vayssierei* Mamet, sp. n. Second stage female.

(ii) *The Second Stage Female* (fig. 2).

Species examined: *C. vayssierei* sp. n.

The second stage female is very similar to that of the first stage but differs in two very conspicuous characters: (*a*) The insect is protected by a scale covering; (*b*) the antennae are very stout and broad and their segmentation is obscure.

Other characters from which this stage can be differentiated from the first lie in its relatively larger size; the more diffuse marginal eyes; the stouter legs in which the trochantero-femoral suture is less marked, and the absence of the long seta which occurs on the submarginal area of the sixth abdominal segment ventrally. In all other characters the second stage female is similar to that of the first stage.

(iii) *The Third Stage Female* (fig. 3).

Species examined : *C. angraeci* Cockerell, *diplothemii* Lepage and Giannotti, *insolitus* sp. n., *vayssierei* sp. n.

The third stage female, which is also protected by a scale covering, is very similar to that of the second stage, except that the prosoma is beginning to show the swollen shape which is one of the characteristics of the adult of certain species. The antennae have lost the stoutness which characterises the second stage and approach in size and segmentation that of the adult ; the legs are relatively smaller than those of the second stage and the marginal eyes have apparently disappeared. All other characters are very similar to those of the second stage.

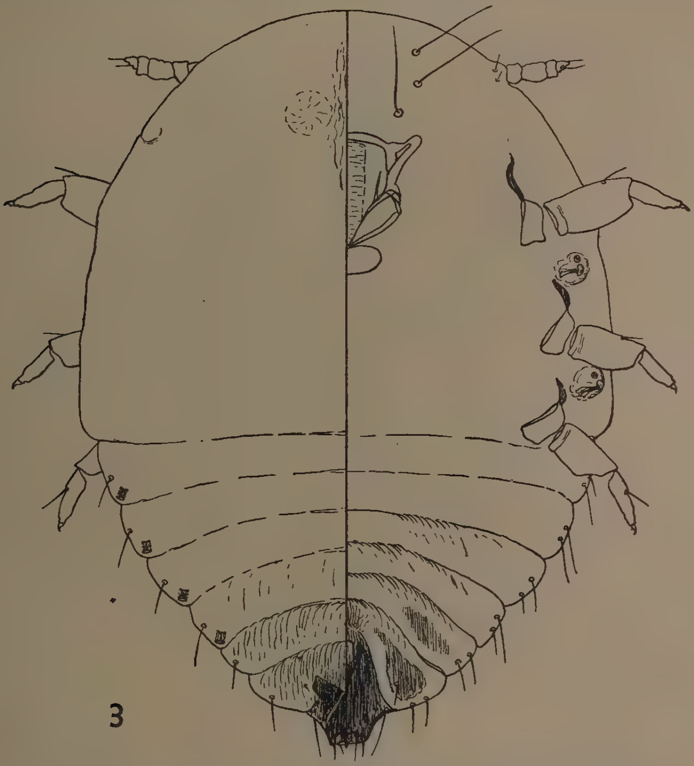

FIG. 3.—*Conchaspis vayssierei* Mamet, sp. n. Third stage female.

This stage, as well as the preceding one, can very readily be differentiated from that of the adult by the complete absence of the ventral metathoracic dermal invaginations. In species in which ventral multilocular pores normally occur in the adult, the absence of such pores is also characteristic of the third stage as well as of the second stage.

3. Morphology of the male stages.

(i) *The First Stage Male* (fig. 1).

It has been found difficult to differentiate between male and female first stage larvae. The characters given above for the first stage female apply also to the first stage male.

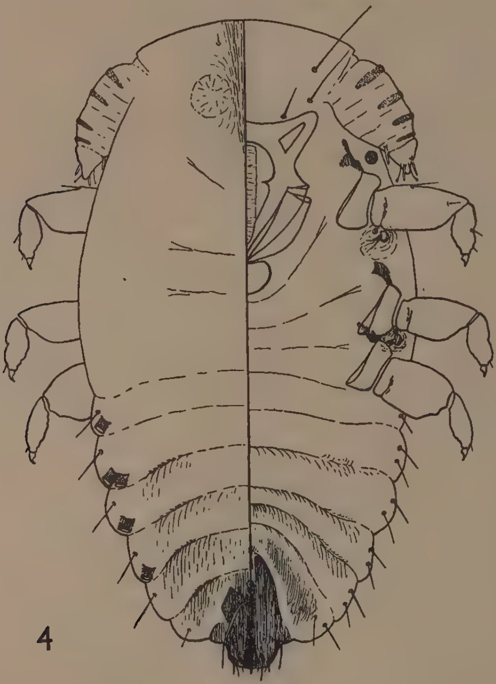

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FIG. 4.—*Conchaspis vayssierei* Mamet, sp. n. Second stage male.

(ii) *The Second Stage Male* (fig. 4).

Species examined: *C. vayssierei* sp. n.

The second stage male is very similar to the first stage in its segmentation and body shape. It differs from that stage by the stouter antennae in which the segmentation is very ill-defined, though sclerotised patches are evident on the external marginal areas. The dorsal ocellar spots are less conspicuous and the true eyes less developed. The mouth-parts are still well-developed and apparently functional. The legs are shorter. The stout, ventral, submarginal seta of the sixth abdominal segment is absent. A feature which may serve to separate this stage from the first stage and from the second stage female lies in the presence of more numerous tubular pores (when these are present) on the anterior abdominal segments marginally. Whether this character holds good for all the species of the genus is uncertain, but in the only species (*C. vayssierei* sp. n.) of which all stages of the male could be studied, the first stage male as well as the first stage female (which are indistinguishable from one another) possess one tubular pore on each lateral margin of the second and third segments only, while the second stage male possesses 1 to 2 tubular pores on the margin of the first four abdominal segments and the second stage female a single pore on each of these four segments.

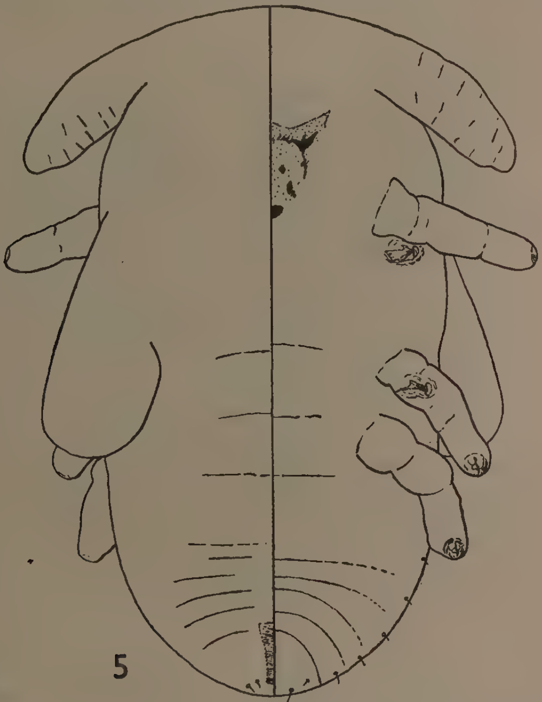


Fig. 5.—*Conchaspis vayssierei* Mamet, sp. n. Third stage male.

(iii) *The Third Stage Male* (fig. 5).

Species examined : *C. vayssierei* sp. n.

In this stage, wing pads begin to make their appearance on the lateral margin of the thorax ; the legs are very different from those of the second stage and no definite division into segments or joints is noticeable in them. However, traces of crease-like segmentation into coxa, trochanter, femur and tibio-tarsus in the leg-buds may be vaguely discerned. The extremities of the legs bear a somewhat sclerotised patch in which a claw is sometimes discernible. The abdominal extremity has lost its characteristic shape and is now rounded. The anus, which in the preceding stages was situated at the apex of the abdomen, is now quite apparent and is located at a short distance from the caudal margin of the body. An anal tube is also fairly conspicuous. The functional mouth-parts are lost and only the interarca and the superarca still persist. The abdomen is devoid of pores and the body setae are much shorter than in the preceding stages. The true eyes and the dorsal ocellar spots have completely disappeared.

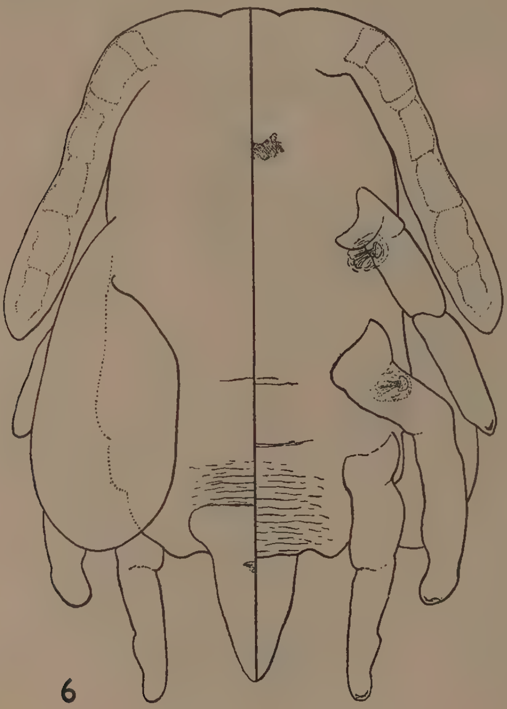


Fig. 6.—*Conchaspis vayssierei* Mamet, sp. n. Fourth stage male.

(iv) *The Fourth Stage Male* (fig. 6).

Species examined: *C. diplothemii* Lepage and Giannotti, *insolitus* sp. n., *socialis* Green, *vayssierei* sp. n.

The legs and wings are much more developed in this stage. The antenna is much longer and that of the adult is discernible within it. The legs show some definite segmentation. The mouth-parts have totally disappeared. The most characteristic feature of this stage is the developing ninth abdominal segment which, after evagination, which occurs during this stage, gives rise to a conical and elongate process which will become the stylus in the adult or fifth stage.

Ventral and dorsal ocelli are found as histoblasts late during this stage.

(v) *The Adult Male* (fig. 7).

Species examined : *C. euphorbiae* Brain, *insolitus* sp. n., *lepagei* Hempel, *socialis* Green, *vayssierei* sp. n.

The body of the adult male is membranous, elongate in outline with the posterior end projecting as a smooth, sclerotic, rapier-like structure. The segmentation of the abdomen is not distinct, except for the posterior segments.

The head, which is broader than long, is separated marginally from the prothorax but is partially fused medially with the bulging part of the thorax. Ventrally it bears medially a pair of ocelli and caudo-laterally dorsally another pair of similar ocelli. Mouth-parts are absent.

The antennae are marginal and vary in size and length. They consist of from 6 to 7 segments. The basal and second segment are globular ; the other segments are more or less elongated and are ornamented with fairly numerous, short and broad spinules with blunt apices. The terminal segment, which is not much elongated and non-annulate, bears in addition to these spinules, four slender and moderately long setae which have knobbed extremities.

The thoracic segments occupy about one-third of the entire length (including stylus) of the whole insect. Their sclerotisation is as shown in the accompanying figure.

The wings are well-developed and possess two prominent veins (the radius and the median) which are united basally over about half their total length. They are provided with a prominent alar lobe near their posterior proximal margin. The halteres are represented by an elongated, fleshy projection of the metathorax. A single seta which is curved at its extremity arises from the distal extremity of each haltere.

The legs are well-developed and subequal in size. The tibia and the tarsus of all legs are fused into a tibio-tarsus which bears numerous short setae. The trochanter is distinct from the femur and bears a minute seta near its distal end. The claw is falcate and is denticulate in only one of the species examined (*insolitus* sp. n). The tibio-tarsal digitules are fairly long and slender, and the ungual digitules, though slender, possess knobbed extremities.

The abdomen is membranous except for the posterior segments. The stylus with its enlarged base appears to constitute the ninth segment ; it is composed of the penis and of the sclerotic genital sheath. The penis, which is clasped by the sheath basally, arises from the swollen base of the ninth abdominal segment and is strongly sclerotic distally. On each side of the stylus and situated on the enlarged base of the ninth segment occurs a moderately long seta.

Pores are totally absent in the adult male.

4. Morphology of the scale of *Conchaspis*.

The scale coverings of the female consist of secretions produced by the underlying insect and are usually circular in outline and conical in shape.

In very few species, the scale is oval in outline and flattened rather than conical. The central part, or " boss," of the conical scales has 6 to 8 ridges or carinae radiating from the apex of the cone to the periphery of the scale itself, or to the periphery of the elevated central portion. Ridges are also present in the flattened scales but are less conspicuous than in the conical ones. The scales are normally felted and white in colour ; sometimes this colour is obscured by dirt or by plant tissues with the result that they appear greyish-white, with sometimes a reddish, yellowish, or brownish tinge. Internally, the scales are

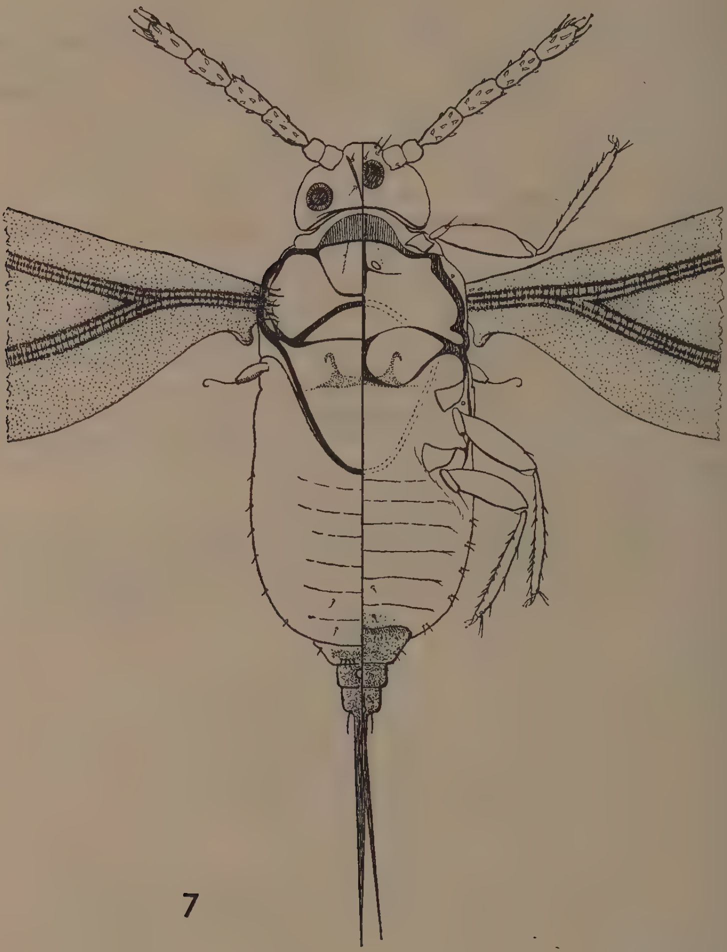


Fig. 7.—*Conchaspis vayssierei* Mamet, sp. n. Adult male.

invariably white, smooth and nacreous. No exuviae are intermingled with these scales.

The male scales are usually of the same colour and texture as those of the females but they are much smaller. They are oblong to oval, flattened and may occur either freely, singly or in masses on the host plant, or under the female scale. The posterior extremity of the male scale has usually a valvular or flap-like opening. A boss is sometimes apparent on these scales but no exuviae are intermingled with them.

The scale coverings of both the female and male of Conchaspidids are very similar to those of the Diaspididae in spite of the fact that no exuviae are intermingled with the secretionary matter forming them. The absence of exuviae can be understood since all the immature stages of both the female and of the male are true limb conservators and that, on moulting, their exuviae, or cast skins, are pushed aside by the active following stage. This process has been observed and is also the case with many other members of the Coccoidea which are limb conservators at all their stages. It has also been observed that the newly hatched female larvae of Conchaspidids do not live under a scale and that once they have selected a convenient spot, they settle there and then cast their skin or moult and the scale covering begins to be formed by the following second stage. The moulting of the second stage occurs under the scale and the second stage exuvium is pushed aside in the scale cavity. This process is repeated until the adult stage is reached. In the male, the process of scale formation is initiated and completed by the second stage. The third and fourth stage males do not seem to play any active part in this process and should be considered as pupal stages.

First stage male larvae after feeding may migrate on to female scales where they moult; the second stage forms the scale there and the complete cycle occurs in this situation. Frequently, several first stage male larvae remain under a female mother scale and undergo their normal development there; as a result, several male scales may be found under a female scale.

In some cases larvae of other insects live as scavengers under the female scales devouring the cast skins and the excrements of the Coccoid. It has been observed that the larva of a Nitidulid beetle lives under the female scales of certain species of Madecassan Conchaspidids, without injuring these Coccoids. It is quite possible that this Nitidulid larva lives both as a predator on the very early stages (eggs and first stage larvae) of the Coccoid and as a scavenger, as noted above. This is supported by the fact that neither eggs, nor newly hatched larvae, nor exuviae of the preceding earlier stages of these Coccoids could be found under the scales harbouring these Coleopterous larvae.

In Ceylon, Green (1896, *Coccidae of Ceylon*, **1** : 22-23) also observed the nearly constant presence of an insect, which he identified as belonging to the Hymenoptera—" presumably the empty pupa of some parasite "—under the scale of the female of *Conchaspis socialis* Green. He also noted that " it is curious, however, that the female Coccid seemed in every case to be uninjured." It would seem that the insect referred to by Green should more appropriately be considered as a scavenger rather than as a parasite or a predator since the presence of cast skins of earlier stages under the scales of the Coccoid was not noticed, though eggs were present under such scales (Green, *loc. cit.*, Plate III, fig. 9).

5. Generic synonym of *Conchaspis*

1893, *Pseudinglisia* Newstead, *Ent. mon. Mag.* **29** : 153 (July). (Type species : *P. rodrigueziae* Newstead.)

Newstead described this genus from specimens, which he named *Pseudinglisia rodrigueziae*, collected on *Rodriguezia secunda*, an Orchid which had been imported in England from Trinidad. Later (1903, *A Monograph of the Coccidae of the British Isles*, **2** : 1), he synonymised *Pseudinglisia* with *Conchaspis* which Cockerell (1893, *Bull. bot. Dep. Jamaica,* **40** : 9 (published March)) had just described from Jamaica.

The type slides of *Pseudinglisia rodrigueziae* Newstead (ex. coll. R. Newstead, in coll. British Museum (Natural History)) have been kindly made available by Mr. J. P. Doncaster, of the Department of Entomology. The author agrees with Newstead that *Pseudinglisia rodrigueziae* is identical with *Conchaspis angraeci* Cockerell, the type of the genus *Conchaspis*. *Pseudinglisia* Newstead is therefore definitely a synonym of *Conchaspis* Cockerell.

6. Composition of the genus *Conchaspis* and Synonymical List of Species.

Twenty-one species are here referred to the genus *Conchaspis ;* of these, twenty have been studied by the author from either type material or from material which can be considered as equivalent to type material.

Two species (*angraeci hibisci* Cockerell and *baiensis* Lepage) are here synonymised, and one (*rodrigueziae* Newstead) has long since been recognised as a synonym of *angraeci* Cockerell.

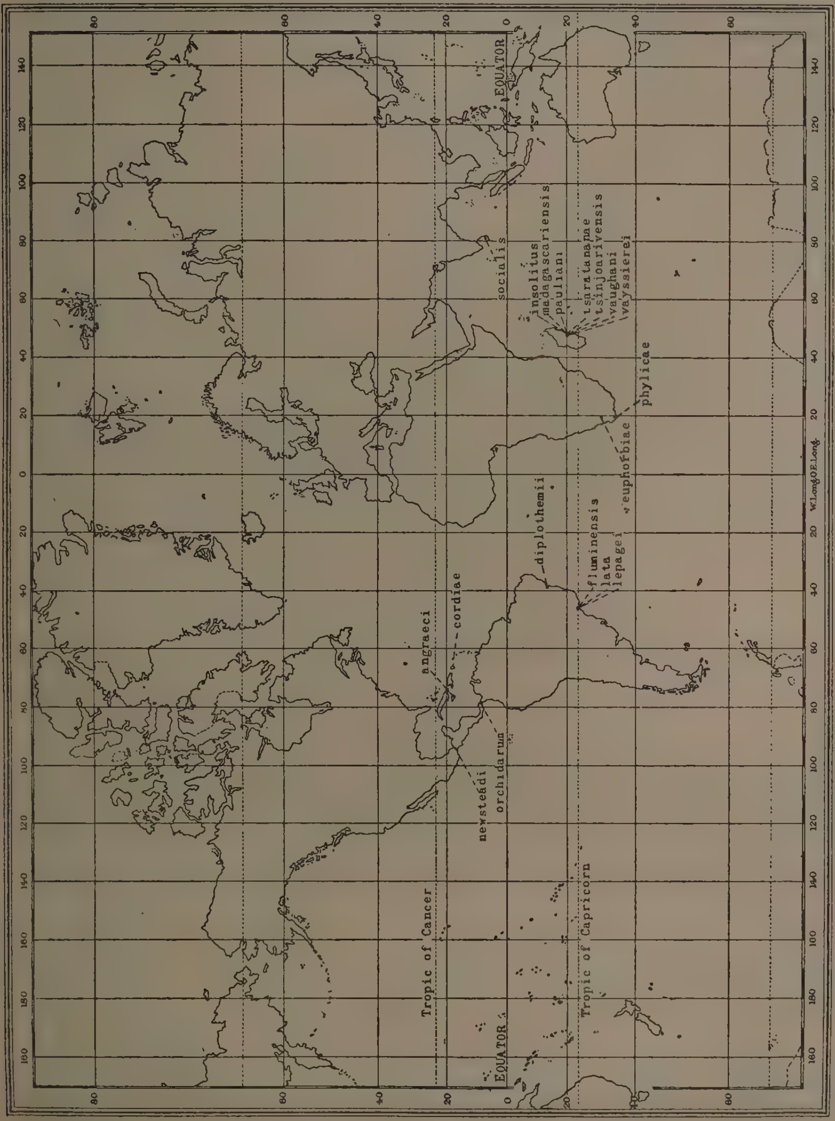
In the following list, names in italics are synonyms of the names in roman type with which they are coupled.

- angraeci Cockerell.
    - *angraeci hibisci* Cockerell.
    - *baiensis* Lepage.
    - *rodrigueziae* Newstead.
- *baiensis* Lepage.
    - angraeci Cockerell.
- cordiae Mamet.
- diplothemii Lepage and Giannotti.
- euphorbiae Brain.
- fluminensis Hempel.
- *hibisci* Cockerell.
    - angraeci Cockerell.
- insolitus Mamet.
- lata Hempel.
- lepagei Hempel.
- madagascariensis Mamet.
- newsteadi Cockerell.
- orchidarum Mamet.
- pauliani Mamet.
- phylicae Mamet.
- *rodrigueziae* Newstead.
    - angraeci Cockerell.
- socialis Green.
- tsaratananae Mamet.
- tsinjoarivensis Mamet.
- vaughani Mamet.
- vayssierei Mamet.

7. Geographical distribution of the genus *Conchaspis*.

The author considers that many members of this genus have yet to be described and that it is accordingly premature to draw conclusions regarding its geographical distribution. It is, however, probable that the range of the genus is restricted to the tropical and subtropical regions.

The accompanying map shows the present distribution of the known species.


EQUATOR
Tropic of Cancer
Tropic of Capricorn
W. Long. 0 E. Long.
socialis
insolitus
madagascariensis
pauliani
tsaratananae
tsinjoarivensis
vaughani
vayssierei
phylicae
euphorbiae
diplothemii
fluminensis
lata
lepagei
angraeci
cordiae
newsteadi
orchidarum

Map showing the geographical distribution of the Genus *Conchaspis* Cockerell.

V. ACKNOWLEDGMENTS.

The author wishes to express his gratitude to Mr. J. P. Doncaster, of the Department of Entomology, British Museum (Natural History), who very kindly made available for study all the species of *Conchaspis* represented in the Coccoid collection of the British Museum, and who generously supplied photostat copies of several publications. His thanks are extended to all those others who have very kindly made available material of *Conchaspis*, particularly to Dr. Harold Morrison, of the Division of Insect Detection and Identification, United States Department of Agriculture; Dr. W. J. Hall, Director of the Commonwealth Institute of Entomology; Dr. H. K. Munro, of the Department of Agriculture, Pretoria, South Africa; Dr. Renaud Paulian Deputy Director of the Institut de Recherche Scientifique, Madagascar; Prof. G. F. Ferris, of the Stanford University, California, U.S.A.; Prof. Paul Vayssière, of the Muséum National d'Histoire Naturelle de Paris, France; Prof. Dr. A. da Costa Lima, of the Escola Nacional de Agronomia, Rio de Janeiro, Brazil, and to Dr. José Pinto da Fonseca, Chefe de Secçao Tecnica Parasitologia Vegetal of the Instituto Biologico, Sao Paulo, Brazil.

Thanks are also due to the Director and Assistant Director of the Institute of Jamaica, to Dr. José Reis, Director da Divisao de Ensino e Documentaçao Cientifica of the Instituto Biologico, Sao Paulo, Brazil, and to Prof. Dr. Hahmann, of the Staatinstitut für Angewandte Botanik, Hamburg, Germany, who very obligingly made available copies of certain important papers connected with this study.

VI. DESCRIPTION OF THE SPECIES OF GENUS *CONCHASPIS.*

Conchaspis angraeci Cockerell (fig. 8).

1893*a*, *Conchaspis angraeci* Cockerell, *Bull. bot. Dep. Jamaica,* **40** : 9, February (published March).
1893*b*, *Conchaspis angraeci* Cockerell, Cockerell, *J. Inst. Jamaica,* **1** : 256, April (published May).
1893*c*, *Conchaspis angraeci* Cockerell, Cockerell, *Gdnrs' Chron.* **13** : 548 (published May).
1893, *Pseudinglisia rodrigueziae* Newstead, *Ent. mon. Mag.* **29** : 153, July.
1895, *Conchaspis angraeci* Cockerell, Cockerell, *Bull. bot. Dep. Jamaica* (N.S.) **2** : 101.
1896*a*, *Conchaspis angraeci* var. *hibisci* Cockerell, *Psyche, Camb., Mass.* **7** (Suppl.) **1** : 19.
1896*b*, *Conchaspis angraeci* var. *hibisci* Cockerell, Cockerell, *Tech. Bull. U.S. Dep. Agric.* **4** : 36.
1903, *Conchaspis angraeci* Cockerell, Fernald, *A Catalogue of the Coccidae of the World* : 38.
1903, *Conchaspis angraeci hibisci* Cockerell, Fernald, *A Catalogue of the Coccidae of the World* : 39.
1903, *Conchaspis angraeci* Cockerell, Newstead, *A Monograph of the Coccidae of the British Isles*, **2** : 3.
1921, *Conchaspis angraeci* Cockerell, MacGillivray, *The Coccidae* : 216.
1921, *Conchaspis angraeci hibisci* Cockerell, MacGillivray, *The Coccidae* : 216.
1939, *Conchaspis baiensis* Lepage, *Arch. Inst. Biol. Def. agric. anim. S. Paulo,* **10** : 314.

Hosts and distribution.—Originally described by Cockerell from *Angraecum eburneum* var. *virens*, JAMAICA : Hope Gardens. Redescribed by Newstead as *Pseudinglisia rodrigueziae*, ENGLAND : Eaton Hall, Chester, from *Rodriguezia secunda*, an orchid freshly imported from Trinidad, xii.1889 and i.1890 (*Mr. C. Hand*). Redescribed by Cockerell (1896 *a.*) as *Conchaspis angraeci* var. *hibisci*, from *Hibiscus* sp., MEXICO : Tamaulipas, 14. x.1894 (*C. H. T. Townsend*, No. 6439). Redescribed by Cockerell (1896b.) as *Conchaspis angraeci var. hibisci*, from *Hibiscus* sp. (probably *floridanus*), MEXICO: Tampico (*Townsend coll.*, No. 28). Redescribed by Lepage as *Conchaspis baiensis*, from *Encyclia* sp., BRAZIL: Bahia, 17.xi.1938 (*H. S. Lepage*).

Dr. Harold Morrison has very kindly made available material of this species from the following hosts and localities: On *Angraecum sesquipedula*, JAMAICA: Hope Gardens (*Dr. Henderson*); on *Codiaeum* sp., PANAMA: Balboa, Canal Zone, 4.iv.1919 (*H. Dietz and I. Molino*, No. G458); on *Coccoloba laurifolia*, MEXICO: Shaw Botanic Gardens, St. Louis, 1.viii.1921 (*W. B. Wood*, No. 8).

Dr. H. Morrison has also kindly informed the author (*in litt.*) that specimens of *angraeci* are represented in the United States National Museum on *Oncidium ampliatum*, from Colombia; on *Oncidium* sp., from Mexico; on *Gongora maculata* and *Epidendrum elongatum*, from Trinidad; on *Cattleya* sp., from Venezuela; on an undetermined orchid, from Nicaragua; on *Oncidium ampliatum* and *Oncidium stipitatum*, from the Canal Zone, Panama; on vanilla, from Ecuador and, on *Cattleya* sp. and *Oncidium* sp., from Brazil.

Specimens of *angraeci* were also kindly made available by Mr. J. P. Doncaster, of the Department of Entomology, British Museum, from the following hosts and localities: On " twigs of unknown tree," DUTCH WEST INDIES: Curaçao, 17.i.1913 (*G. E. Bodkin*), det. R. Newstead; on *Stephanotis* sp., WEST INDIES: Barbados (*J. R. Bovell*, I.B.E. No. 47), det. E. E. Green.

Dr. A. da Costa Lima has kindly made available unmounted material of this species, identified as "*Conchaspis baiensis* Lepage," from *Acalypha* sp., Universade Rural, Kilometre 47, road from Rio to Sao Paulo, Brazil, viii.1948, E. Arrunda collector, entered under No. 10122 in the collection of the Escola Nacional de Agronomia, Rio de Janeiro, Brazil.

Dr. W. J. Hall, of the Commonwealth Institute of Entomology, also kindly made available mounted individuals of "*Conchaspis baiensis* Lepage," on *Acalypha* sp., from Brazil, from named material received by him from Dr. A. da Costa Lima.

Habit.—Occurring on stems and leaves of host plants.

Scale of female described by Newstead (1903) as " . . . approximately circular, somewhat conical, apex bluntly pointed, margins broad and flat; radiating from the apex are from six to eight ridges or carinae, many of which disappear before reaching the centre between the apex and margin. White, sub-opaque, the spaces between the carinae and sometimes irregular bands beyond them, darker, and of a more glass-like texture . . . wide, 2–2·25 mm.; high, 0·50–1 mm."

Scale of male not observed.

Recognition characters.—Adult female elongate oval. Prosoma not swollen. Derm very finely stippled, membranous except from the third abdominal segment to the posterior apex which shows some sclerotisation. Antenna 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with a few fine creases radiating from the central area. Length, about 1·2 mm.

Dorsal tubular ducts entirely absent.

Ventral multilocular pores present in a submarginal group, a submedian group and a group intermediate between the submarginal and the submedian groups on the third and fourth abdominal segments, and in a submarginal group on the fifth segment. One pore very occasionally occurring on the second segment submarginally and in the intermediate position. The submarginal groups of the third, fourth and fifth segments composed of 2–6 pores, 1–5 pores and 1–3 pores respectively; the intermediate groups of the third and fourth segments with 1–3 and 0–2 pores respectively; the submedian groups of the third and fourth segments with 1–4 and 0–2 pores respectively. The submarginal, intermediate and submedian groups of the fourth segment sometimes merge into one another so as to form an almost continuous series.

Abdominal tubercles with rounded apices occurring on the first five segments submarginally, one per segment. Metathoracic dermal invaginations large, slightly sclerotised.

First stage larva: Body elongate oval; derm a little sclerotised, very finely stippled. Antennae 6-segmented, with terminal segment longest and bearing several setae. Eyes submarginal. Dorsal ocellar spots very weakly marked. Dorsal tubular pores entirely

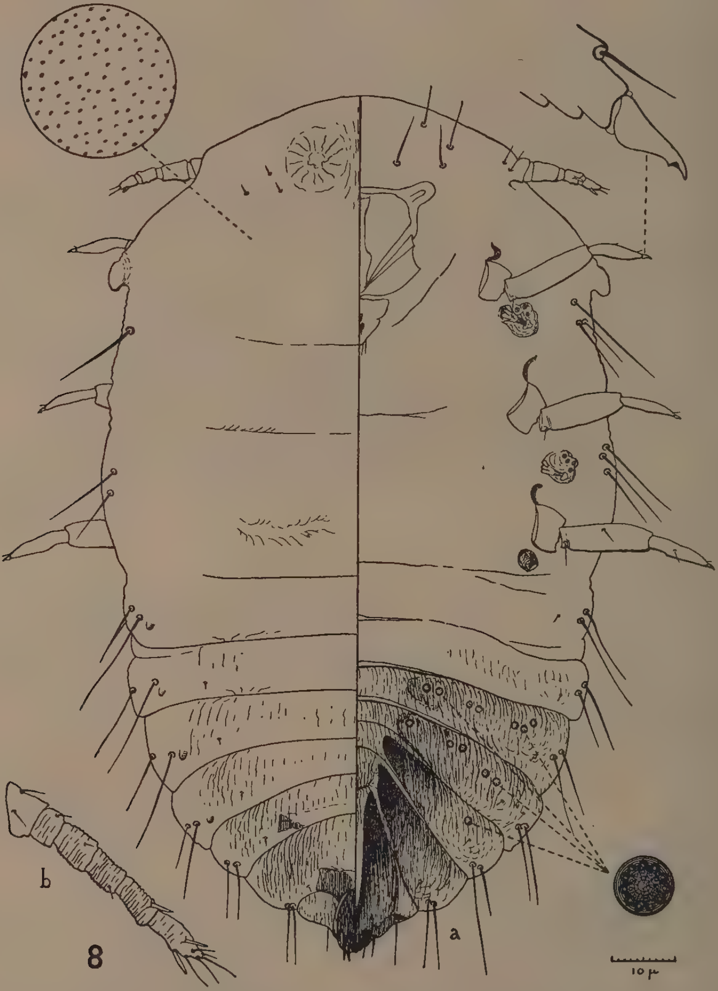


Fig. 8.—*Conchaspis angraeci* Cockerell. *a*, Adult female; *b*, antenna of first stage larva.

lacking. Abdominal tubercles with rounded apices, occurring on the second to the fifth segments submarginally, one per segment. Length, about 0·3 mm.

Notes.—*Conchaspis angraeci hibisci* Cockerell is synonymised here with *C. angraeci* Cockerell (**syn. nov.**) after an examination of the type slides (of both) which were kindly made available by Dr. Harold Morrison.

Lepage (1939) described *Conchaspis baiensis* on the assumption that the figure published by Newstead (1903) represented *C. angraeci* Cockerell. After studying a type specimen of *Pseudinglisia rodrigueziae* Newstead, which Newstead (1903) synonymised with *C. angraeci* after comparison with specimens of the latter which he had received from Cockerell (Cockerell, 1895), the author is fully satisfied that Newstead's figure of *C. angraeci* (1903) is erroneous and does not represent either *C. angraeci* or *P. rodrigueziae*. Quite authentic material of *C. baiensis* Lepage from Brazil have been found to agree in all respects with typical *angraeci* and with material of this species from other localities of Central America and the West Indies. *C. baiensis* Lepage is therefore considered a synonym of *angraeci* Cockerell (**syn. nov.**).

The accompanying figure is based upon specimens from the type material.

Conchaspis cordiae sp. n. (fig. 9).

Hosts and distribution.—Type and paratypes from "black sage" (*Cordia* sp.), West Indies : Shoys, St. Croix, Virgin Islands, 26.vii.1919 (*C. E. Wilson*, No. 5), another paratype from "Mahogany," same locality, 10.vi.1917 (*H. Morrison*, No. 158).

Habit.—Occurring on twigs of hosts.

Scale of female almost circular, white, sometimes obscured with greyish-brown extraneous particles, moderately convex, without marked ridges radiating from the central apical area, occurring singly or in small masses, compact in texture ; white-nacreous internally. Diameter, about 2 mm.

Recognition characters.—Adult female elongate oval ; prosoma very slightly swollen ; derm membranous, very finely stippled. Antennae 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with a few creases radiating from the central area. Length, about 1·0 mm.

Dorsal tubular ducts small, occurring in small groups on the metathorax and first three abdominal segments marginally or submarginally : metathoracic group consisting of 1 pore and the groups of the first, second and third abdominal segments of 1–4, 1–4 and 0–1 pores respectively.

Ventral multilocular pores occurring in a submarginal group, a submedian group and a group intermediate between the submarginal and submedian groups on the third and fourth abdominal segments and in a submarginal group only on the fifth segment ; the submarginal groups of the third, fourth and fifth segments consisting of 1–4, 2–3 and 0–1 pores respectively ; the intermediate groups of the third and fourth segments of 0–2 pores respectively, and the submedian groups of the same segments (3rd and 4th) of 0–1 pore respectively.

Ventral abdominal tubercles with smooth or finely rugose apices, present on the first to the fourth segments submarginally. The occurrence of tubercles on the fifth segment is variable. Metathoracic dermal invaginations large, slightly sclerotised.

Notes.—Specimens of this species were kindly made available by Dr. Harold Morrison.

The type and paratypes have been deposited in the Coccoid collection of the United States National Museum, Washington, D.C.; other paratypes are in the Stanford University Natural History Museum, California, the British Museum (Natural History), and in the author's collection.

The accompanying figure is based upon "type" material from "black sage."

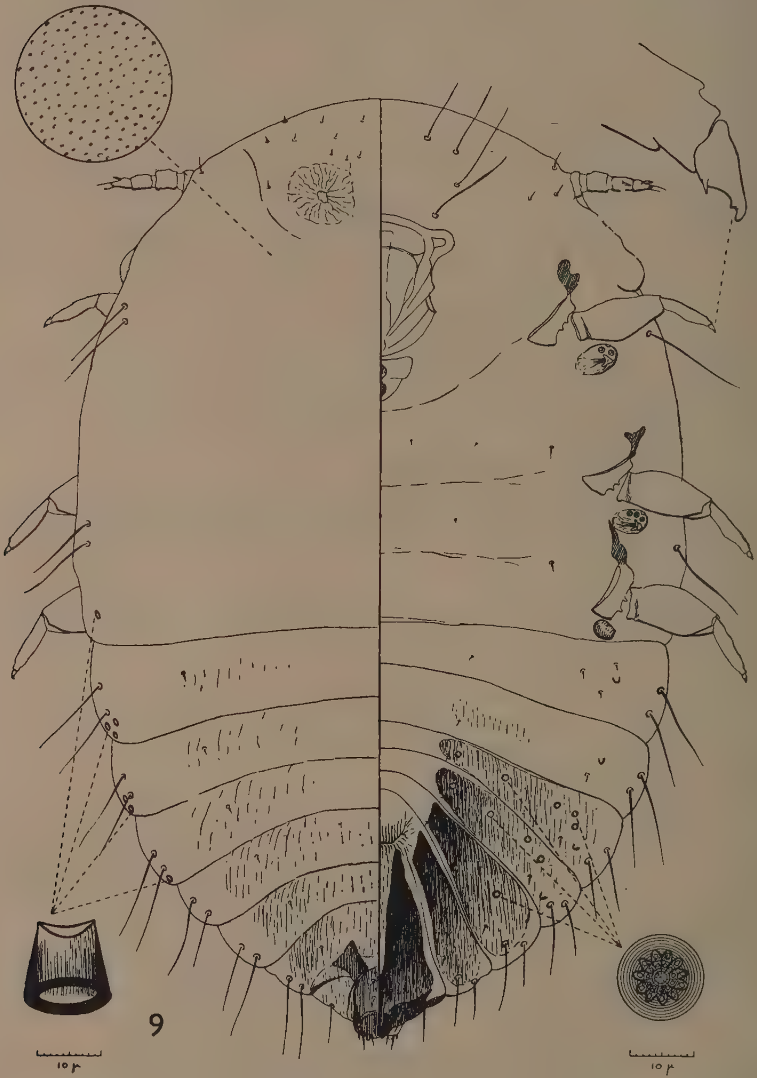


FIG. 9.—*Conchaspis cordiae* Mamet, sp. n. Adult female.

Conchaspis diplothemii Lepage & Giannotti (fig. 10).

1943, *Conchaspis diplothemii* Lepage and Giannotti, *Arch. Inst. biol. Def. agric. anim., S. Paulo*, **14** : 346.

Host and Distribution.—Originally described from *Diplothemium condescens* Mart., BRAZIL : Bahia (*G. Bondar*), v.1941.

Habit.—Occurring on the undersurface of leaves of host.

Scale of female almost circular, very slightly convex, of felted texture, completely obscured by the thick, straw-coloured tomentum of the undersurface of the leaves of the host ; pure white and nacreous internally. Diameter, about 3 mm.

Scale of male elongate, pure white, felted, occurring in small clusters under the female mother scale.

Recognition characters.—Adult female elongate ; prosoma not swollen ; derm membranous, very finely stippled. Antennae 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with a few fine creases radiating from the central area. Length, about 1·0 mm.

Dorsal tubular ducts large, occurring in marginal and submarginal groups on the metathorax and first four abdominal segments, as follows : metathoracic group with 2–3 pores ; groups of the first, second, third and fourth abdominal segments each with 4–6, 3–6, 3–5 and 2–4 pores respectively.

Ventral multilocular pores occurring singly on the second to the sixth abdominal segment submarginally.

Metathoracic dermal invaginations large, slightly sclerotised.

First stage larva : Body elongate oval ; derm a little sclerotised, very finely stippled. Antennae 6-segmented ; terminal segment a little longer than third segment, bluntly pointed at its extremity which bears a seta, with, at about the middle of its length, a protuberance bearing an apical seta ; fourth and fifth segments together a little longer than the sixth segment. Eyes submarginal. Dorsal ocellar spots very weakly marked. Dorsal tubular pores small, occurring as follows : two on the margin of each of the first and second segments of the abdomen, and only one on the margin of the third segment. Length, about 0·3 mm.

Notes.—Through the kindness of Prof. A. da Costa Lima, it has been possible to examine material from the collection of the Escola Nacional de Agronomia, Rio de Janeiro, No. 10090, from *Diplothemium condescens*, from Bahia, Brazil (ex coll. Lepage and Giannotti) and bearing the same data as the type. Also, Dr. J. Pinto da Fonseca has kindly made available Brazilian material of the same species from the collection of the Instituto Biologico, Sao Paulo (host and other data not mentioned), which compares very well with the authentic material mentioned above. It is on this material that the above redescription and the accompanying figure are based.

The constant presence of a marginal or submarginal group of tubular pores on the metathorax at once differentiates *C. diplothemii* Lepage and Giannotti from the closely related *C. lepagei* Hempel.

Conchaspis euphorbiae Brain (fig. 11).

1918, *Conchaspis euphorbiae* Brain, *Bull. ent. Res.*, **9** : 113.

Hosts and distribution.—Originally described from " melkbosch " (*Euphorbia* sp.), SOUTH AFRICA : Concordia, Namaqualand (*Mr. Krapohl*), (Brain Coll., Nos. 13 and 14). Material collected on *Euphorbia* sp., at Worcester, Cape Province, South Africa, by A. Fouché, No. Ac. P.4359, has also been examined.

Habit.—Occurring on twigs of host.

Scale of adult female described by Brain as " . . . large, reaching 6·5 mm. for its greatest diameter, average size about 5 mm., nearly circular, sometimes slightly elongate, moderately arched. Colour white, but appearing greyish owing to the presence of dark particles incorporated in it, especially at the margins of the component lamellae. The scale is somewhat flattened on top, where it usually presents a more or less irregular, central

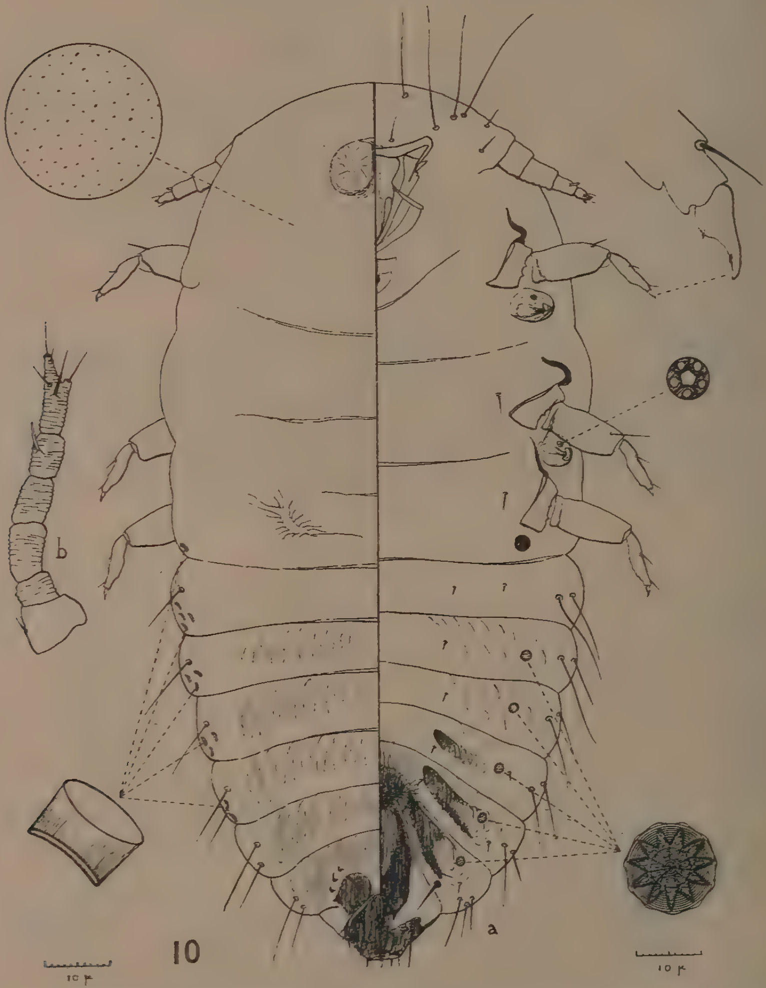


Fig. 10.—*Conchaspis diplothemii* Lepage & Giannotti. *a*, Adult female; *b*, antenna of first stage larva.

yellowish projection surrounded by a concentric ring. In texture, the scale is compact, the main dome being slightly roughened above and shiny beneath." . . . "Large numbers of scales are often aggregated into masses which entirely surround the smaller twigs of the host plant."

Scale of male elongate, white, sometimes occurring in fairly large clusters on female scales.

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen; derm slightly sclerotised, finely stippled. Antennae 3-segmented; sensory hair of second segment very broad, more or less elongate-conical. Dorsal ocellar spots very

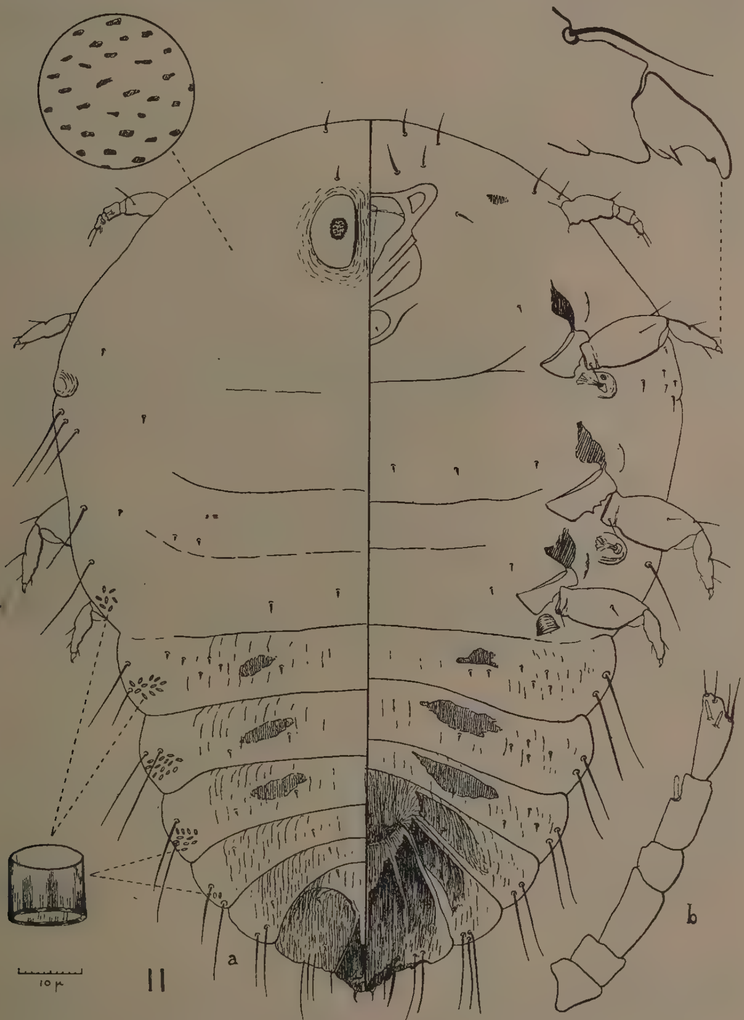


FIG. 11.—*Conchaspis euphorbiae* Brain. Adult female.

conspicuous, represented as clear discs, each with central area sclerotised and circumscribed by a narrow, highly sclerotised rim. Length, about 1·7 mm.

Dorsal tubular ducts small, occurring in marginal or submarginal groups on metathorax and first four abdominal segments, as follows : metathoracic group with 6–9 pores ; groups of first, second, third and fourth segments with 11–16, 10–14, 5–11 and 0–2 pores respectively.

Ventral multilocular pores absent.

Metathoracic dermal invaginations fairly large and sclerotised.

First stage larva : Body elongate oval ; derm a little sclerotised, finely stippled. Antennae 6-segmented ; third and fifth segments subequal and each a little longer than the sixth ; fourth segment globular. Eyes submarginal. Dorsal ocellar spots conspicuous, represented as clear discs with a few creases. Dorsal tubular pores absent. Length, 0·3 mm.

Notes.—The above redescription and the accompanying figures are based upon specimens from *Euphorbia* sp., Worcester, Cape Province, South Africa, March, 1939, F. A. Fouché collector, No. Ac.P.4359, kindly made available by Dr. H. K. Munro and Dr. W. J. Hall.

Brain (1918), in describing *C. euphorbiae*, mentions that the collection numbers of this species are 13 and 14. Only six slides bearing No. C.K.B.14 are to be found in the Brain collection at the Department of Agriculture, Pretoria, South Africa. Three of them, bearing data similar to those mentioned in the original description of the species, have been made available by Dr. H. K. Munro. It is here assumed that they constitute part of the " type material " of the species. As they have not been marked by Brain as belonging to this " type material," I have, on the suggestion of Dr. Munro, designated one slide as " lectotype " and the others as " lectoparatypes."

The " lectotype " and a " lectoparatype " are in the Brain collection of Coccoidea, at the Department of Agriculture, Pretoria, South Africa, and the other " lectoparatype" in the author's collection.

Named mounted individuals from the material from Worcester, Cape Province, South Africa, compared with the " lectotype " material have been deposited in the collection of the British Museum (Natural History), the United States National Museum, the Muséum National d'Histoire Naturelle de Paris, the Stanford University Natural History Museum, California, and in the Coccoid collection of the Department of Agriculture, Pretoria, South Africa, and in that of the author.

Conchaspis fluminensis Hempel.

1904, *Conchaspis fluminensis* Hempel, *Bol. Agric., S. Paulo,* 5 : 312.

Host and Distribution.—Originally described from a sylvan shrub, Brazil : Itatiaya, Morro dos Papagaios, No. 81–82.

Habit.—Occurring on leaves of host.

Original description.—The original description of this species is here presented verbatim :

" O escudo da femea é mais ou menos circular, até 1·30 mm. de diametro, de côr branca, duro, feltroso por fóra, liso e branco por dentro, e com o dorso um pouco convexo. O escudo ventral consiste en uma escama fina e branca que fica ligada na superficie da folha.

" A femea é de côr amarello-clara, com as extremidades das pernas e das antennas mais escuras. O corpo é curto e robusto tendo 0·56 mm. de comprimento e 0·45 mm. de largura. O abdomen é mais largo que a cabeca e o thorax. As antennas tem cinco articulações e sao grossas e curtas, tendo apenas 219 microns de comprimento. O comprimento das articulações, en *microns*, é o seguinte (1) 36 ; (2) 20 ; (3) 92 ; (4) 28 ; (5) 43.

As duas ultimas articulaçeõs são escuras, e a ultima têm na ponta dois pellos compridos e grossos. As pernas são curtas et grossas com duas unhas cada uma. Não ha articulação entre o tarso e a tibia. Ha um espinho curto e grosso na tibia, perto da extremidade ; e ha tambem dois digitulos compridos e finos com as extremidades curvadas, na tibia, e nas unhas ha dois digitulos curtos e largos. No lado ventral, perto da extremidade anterior, ha dois pellos muito compridos e grossos. Os segmentos do abdomen são bem visiveis. Ha, no ultimo segmento, dois pequenos logares espessos como glandulas, e mais duas àreas glandulosas, irregulares, no lado inferior, e no lado superior, tanbem, duas àreas irregulares. O ultimo segmento termina em dois pares de lôbos, sendo o par mediano o maior. Ha tambem no abdomen, perto das margens, diversos pellos grandes e outros menores."

Notes.—Specimens of this species have not been available. It is not possible, in view of the incompleteness of this description, which was not accompanied by figures, to be certain of the identity of this species. However, assuming that the description, as far as the characters mentioned therein are correct, *fluminensis* is perhaps separable from the other known species of *Conchaspis* by its 5-segmented antennae.

Conchaspis insolitus sp. n. (fig. 12).

Hosts and distribution.—Type from *Euphorbia larro*, MADAGASCAR : Lake Tsimanampetsotsa, v.1951 (*R. Paulian*, No. 404). Paratype from *Euphorbia stenoclada*, from Tuléar, Madagascar, vi. 1951 (*R. Paulian*, No. 426).

Habit.—Occurring on stem of host.

Scale of female almost circular, roundly convex, of somewhat hard, felted texture, white, outer surface usually coated with pale yellowish glassy secretions produced by the host. Internally, the scale is pure white and a little shiny. Diameter, about 4 mm.

Scale of male elongate oval, of same texture as that of female, white in colour. Length, about 2 mm.

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen ; derm slightly sclerotised, finely stippled. Antennae 2-segmented. Dorsal ocellar spots small, represented as clear discs with central area sclerotic and circumscribed by a more sclerotised rim. A few, short, well sclerotised, transverse creases occurring on the frontal area dorsally. Length, about 1·5 mm.

Dorsal tubular pores absent.

Ventral multilocular pores occurring submarginally on the first, second and third abdominal segments in groups of 3–4, 3–4, and 2–3 respectively. Ventral multilocular pores also occur on the head and the three thoracic segments submarginally : on the head, 2–8 such pores occur at about midway between the antennal bases and the mouth-parts ; on the prothorax, 2–11 pores occur in a position intermediate between the insertion of the legs and the margin ; and, on the meso- and the metathorax, these pores occur closer to the spiracles than to the margin and number between 3–5 and 4–5 in each position.

Metathoracic dermal invaginations small, slightly sclerotised.

Notes.—This species is remarkable by the occurrence of multilocular pores on the prosomatic segments. In this character, it departs from all the other known species of the genus and is therefore easily recognisable.

The type and paratype are in the author's collection.

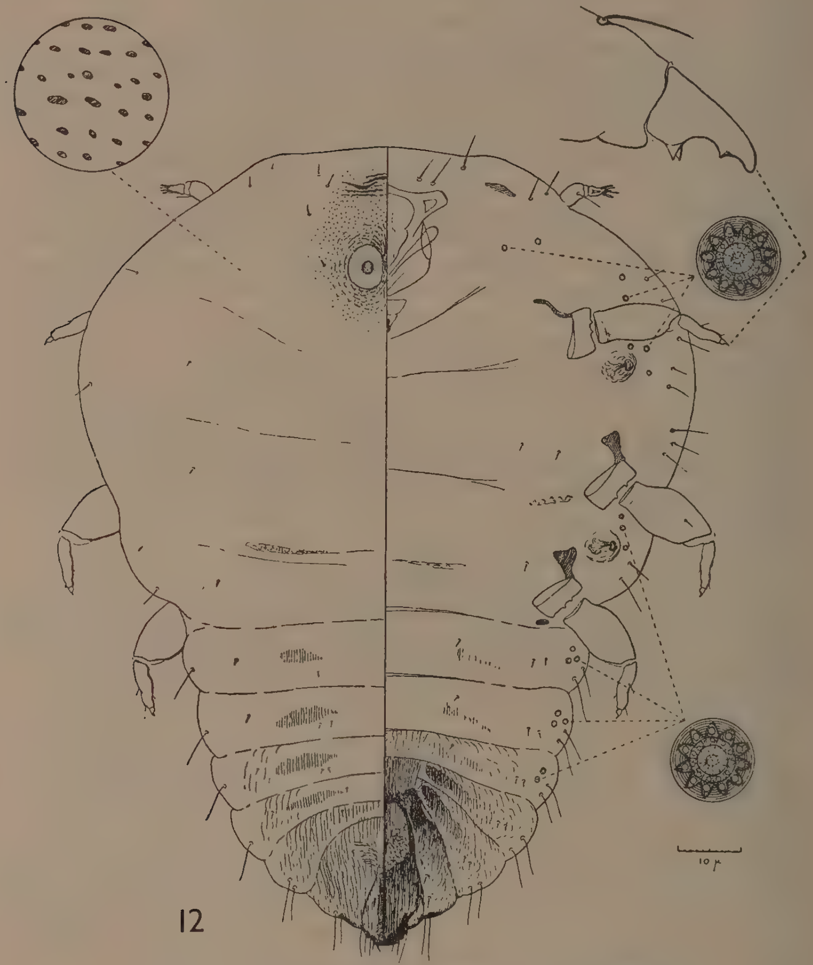


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Fig. 12.—*Conchaspis insolitus* Mamet, sp. n. Adult female.

Conchaspis lata Hempel (fig. 13).

1937, *Conchaspis lata* Hempel, *Arch. Inst. biol. Def. agric. anim. S. Paulo*, **8** : 21.

Host and distribution.—Originally described from an undetermined tree, Brazil : Rio de Janeiro, and entered under No. 104 in the collection of the Instituto Biologico, Sao Paulo, Brazil.

Specimens from undetermined host, from Rio de Janeiro, Brazil, and bearing No. 8670 of the collection of the Escola Nacional de Agronomia, Rio de Janeiro, received from Prof. A. da Costa Lima, and other specimens from undetermined host, from Brazil, received from Dr. J. Pinto da Fonseca, of the Instituto Biologico, Sao Paulo, have been studied.

Habit.—Occurring on bark of host.

Scale of female circular, slightly convex, compact in texture, white, nearly always obscured by the buff to dark-reddish particles of bark of host. Diameter, about 4 mm. Internally, the scale is smooth, white-nacreous, with buff markings due to particles of bark of host. The scales generally overlap one another and are aggregated into small masses.

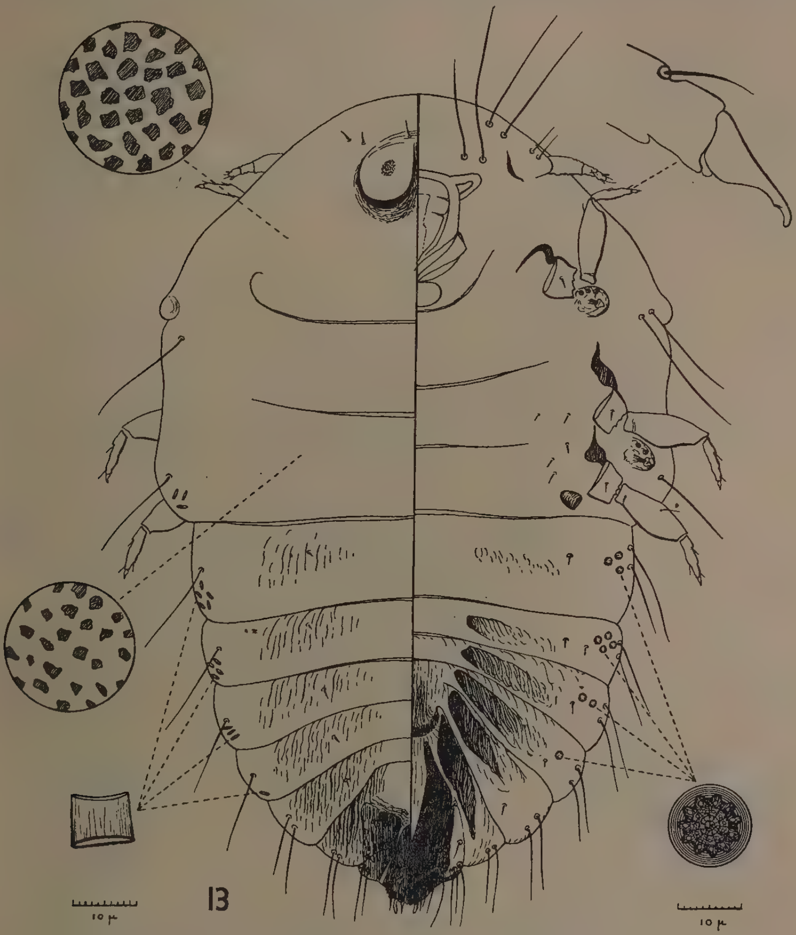

Fig. 13.—*Conchaspis lata* Hempel. Adult female.

Scales of males usually occurring in small groups on scales of females, elongate, of the same texture and colouration as that of female ; length, about 2 mm.

Recognition characters.—Adult female of the shape common to the genus ; derm slightly sclerotised, coarsely stippled. Antennae 3-segmented. Dorsal ocellar spots very conspicuous, with margin well-sclerotised posteriorly and open anteriorly. Length, about 1·1 mm.

Dorsal tubular ducts small, occurring in marginal or submarginal groups on metathorax and first four abdominal segments as follows: metathoracic group with 2–5 pores; groups of the first, second, third and fourth segments with 3–5, 2–5, 2–4 and 1 pores respectively.

Ventral multilocular pores occurring submarginally on first to fourth abdominal segments in groups of 2–4, 3–4, 2–3, and 0–2 pores respectively.

Metathoracic dermal invaginations fairly large and sclerotised.

Notes.—This species is related to *C. socialis* Green from which it can at once be distinguished by the structure of the dorsal ocellar spots, the stippling of the derm, the size of the dorsal tubular pores, and the fewer multilocular pores on the abdominal segments.

The above redescription and the accompanying figure are based upon specimens from undetermined host, from Brazil, ex coll. Instituto Biologico, Sao Paulo, Brazil.

Conchaspis lepagei Hempel (fig. 14).

1937, *Conchaspis lepagei* Hempel, *Arch. Inst. biol. Def. agric. anim. S. Paulo*, **8**: 23.

Host and distribution.—Originally described from *Atrocaryum ayri* Mart. from Brazil: Santos.

Habit.—Occurring on the undersurface of leaves of host, usually along the veins.

Scale of female semi-transparent, white, flat, elongate-oval, closely felted in texture, occurring singly or aggregated into small elongated masses in which the scales overlap one another; sometimes adpressed along the veins of the leaves of the host with the result that the side adjoining the leaf veins becomes straight. Length, about 5·5 mm.

Scale of male elongate, white, occurring in small clusters under female scale.

Recognition characters.—Adult female elongate, prosoma not swollen; derm membranous, stippling not apparent. Antennae 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with fine creases radiating from central area. Length, about 0·8 mm.

Dorsal tubular ducts large, occurring in marginal or submarginal groups on the first four abdominal segments, as follows: first segment with a group of 1–3 pores; second segment with 2–4 pores; third and fourth segments each with 1–3 pores. Ducts are completely lacking on the metathorax submarginally.

Ventral multilocular pores large, occurring singly on each of the second to sixth abdominal segments submarginally.

Metathoracic dermal invaginations somewhat small, slightly sclerotised.

First stage larva: Body elongate-oval; derm a little sclerotised, very finely stippled. Antennae 6-segmented; terminal segment as in *C. diplothemii*. Eyes submarginal. Dorsal ocellar spots fairly conspicuous, represented as clear discs with a few creases. Dorsal tubular pores large, occurring singly on the margin of each of the first three abdominal segments. Length, 0·3 mm.

Notes.—This species is very closely related to *C. diplothemii* Lepage and Giannotti, from which it differs by the absence of tubular pores on the metathorax submarginally.

The above redescription and the accompanying figures are based upon specimens from a palm, Santos, Brazil, 7.xii.1934 (*H. S. Lepage*), No. E.E.G.

26/35, now in the Green collection of Coccoidea in the British Museum, kindly made available by Mr. J. P. Doncaster.

Other specimens made available by Dr. J. Pinto da Fonseca, of the Instituto Biologico, Sao Paulo, Brazil, have also been examined.

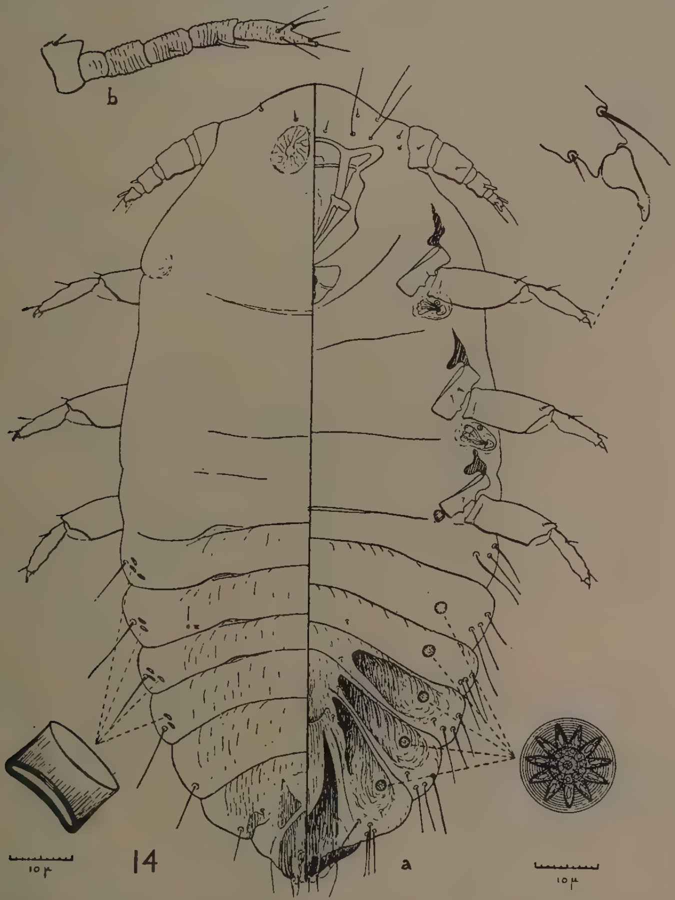

FIG. 14.—*Conchaspis lepagei* Hempel. *a*, Adult female ; *b*, antenna of first stage larva.

Conchaspis madagascariensis sp. n. (fig. 15).

Host and distribution.—Type and paratypes from " Amborasaha," MADAGASCAR : Périnet, 26.v.1950 (*A. Robinson*, No. 188).

Habit.—Occurring on the undersurface of leaves of host.

Scale of female circular, white, moderately convex, semi-transparent marginally, opaque in the area occupied by the centrally placed boss which is conical and radially ridged ; occurring singly. Diameter, about 1·5 mm.

Scale of male not seen.

Recognition characters.—Adult female somewhat of the shape common to the genus, with prosoma a little swollen; derm membranous, very finely stippled. Antennae 4-segmented. Dorsal ocellar spots membranous, with no trace of sclerotisation, with a few fine creases radiating from the central area. Length, about 0·8 mm.

Dorsal tubular ducts small, occurring in marginal or submarginal groups on metathorax and first four abdominal segments, as follows: metathoracic group with 2–4 pores; first, second, third, and fourth abdominal segments each with a group of 5–8, 5–7, 5–9, and 3–5 pores respectively.

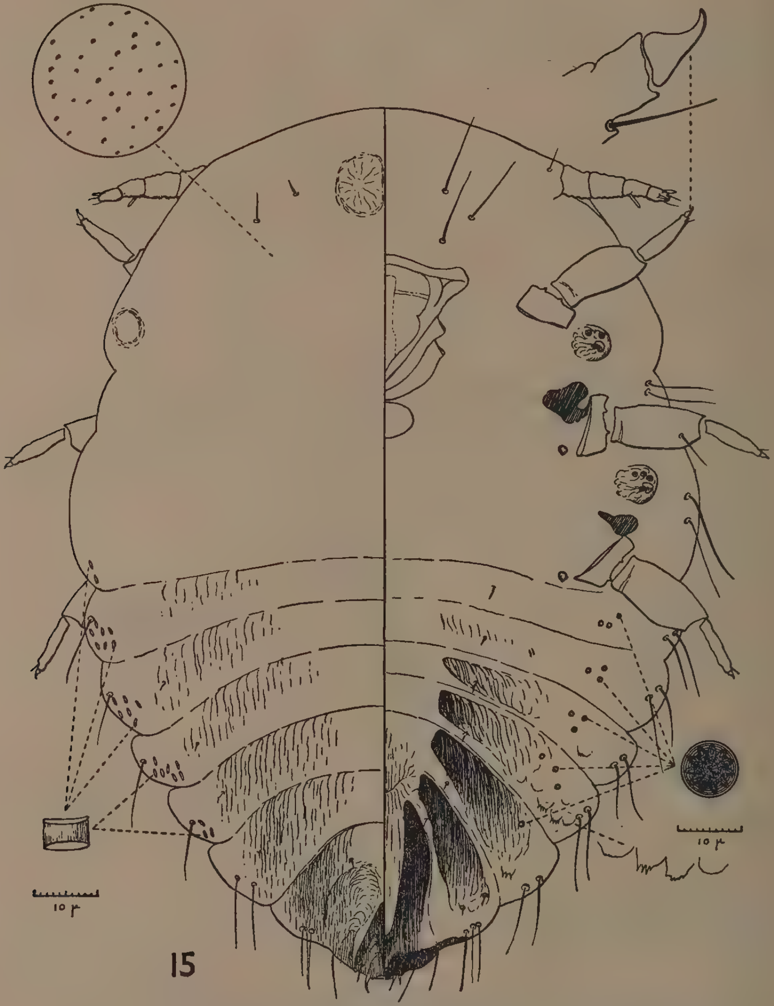

FIG. 15.—*Conchaspis madagascariensis* Mamet, sp. n. Adult female.

Ventral multilocular pores occurring in submarginal groups on the first to the fifth abdominal segments, as follows: first segment with 1–3 pores; second segment with 2–3 pores; third segment with 2–4 pores; fourth segment with 1–3 pores, and fifth segment with 0–3 pores.

Abdominal tubercles with swollen base and with apices either smooth, finely serrated or deeply incised, occurring singly or in groups of 2–4 on the third to the fifth segments submarginally. Ventral thoracic dermal invaginations small, slightly sclerotised; one pair occurring on the mesothorax and another pair on the metathorax.

Notes.—*C. madagascariensis* is at once separable from all the known species of the genus by the occurrence of a pair of ventral dermal invaginations on the mesothorax.

The type and paratypes are in the author's collection. Other paratypes have been deposited in the collection of the British Museum (Natural History), the United States National Museum, the Muséum National d'Histoire Naturelle de Paris, the Stanford University Natural History Museum, and in that of the Institut de Recherche Scientifique de Madagascar.

Conchaspis newsteadi Cockerell (fig. 16).

1897, *Conchaspis newsteadi* Cockerell, *Canad. Ent.*, **29** : 270.
1903, *Conchaspis newsteadi* Cockerell, Fernald, *Catalogue of the Coccidae of the World* : 39.
1921, *Conchaspis newsteadi* Cockerell, MacGillivray, *The Coccidae* : 215.

Hosts and distribution.—Originally described from "Zuchil tree" (*Plumeria* sp.), MEXICO : Vera Cruz, 26.ii.1896 (*Townsend*, No. Div. Ent. 7159).

Material of this species from "Rosa Maria," from Mexico, misidentified by E. E. Green, as "*Conchaspis angraeci* var. *hibisci* Cockerell," and also other individuals from "Frangipani" (*Plumeria* sp.), from Vera Cruz, Mexico (ex coll. E. E. Green), have been examined.

Habit.—Described as occurring on the bark of the host.

Scale of female described by Cockerell as ". . . overlapping; subcircular to oval, dirty white, low conical, diameter 2·5 mm. Apex sublateral, no radiating ridges."

Scale of male described by Cockerell as ". . . similar to that of the female in texture, but small and elongate."

Recognition characters.—Adult female elongate oval, with prosoma not swollen; derm finely stippled, membranous except from the second abdominal segment to the posterior apex which is somewhat sclerotised. Antennae 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with a few creases radiating from the central area. Length, about 1·1 mm.

Dorsal tubular ducts entirely absent.

Ventral multilocular pores occurring in a submarginal group, a submedian group, and a group intermediate between the submarginal and submedian groups on the third and fourth segments of the abdomen; in a submarginal and an intermediate group on the second segment, and in a submarginal group on the fifth segment. The submarginal groups of the second to fifth segments composed of 1–5, 2–7, 2–5, and 1–3 pores respectively; the intermediate groups of the second to fourth segments composed of 1–2, 1–3, and 1–3 pores respectively, and the submedian groups of the third and fourth segments each composed of 1–2 pores. The submarginal, intermediate, and submedian groups of pores of the third and fourth segments sometimes merge into one another so as to form an almost continuous series.

Abdominal tubercles with rounded apices, occurring on the first five segments submarginally, one per segment. Metathoracic dermal invaginations large and slightly sclerotised.

Notes.—*Conchaspis newsteadi* differs from *C. angraeci* Cockerell by the occurrence of a group of multilocular pores in each of the submarginal and intermediate areas of the second abdominal segment in the adult female.

The figure accompanying the above redescription is based upon "type" material of this species, kindly made available by Dr. Harold Morrison.

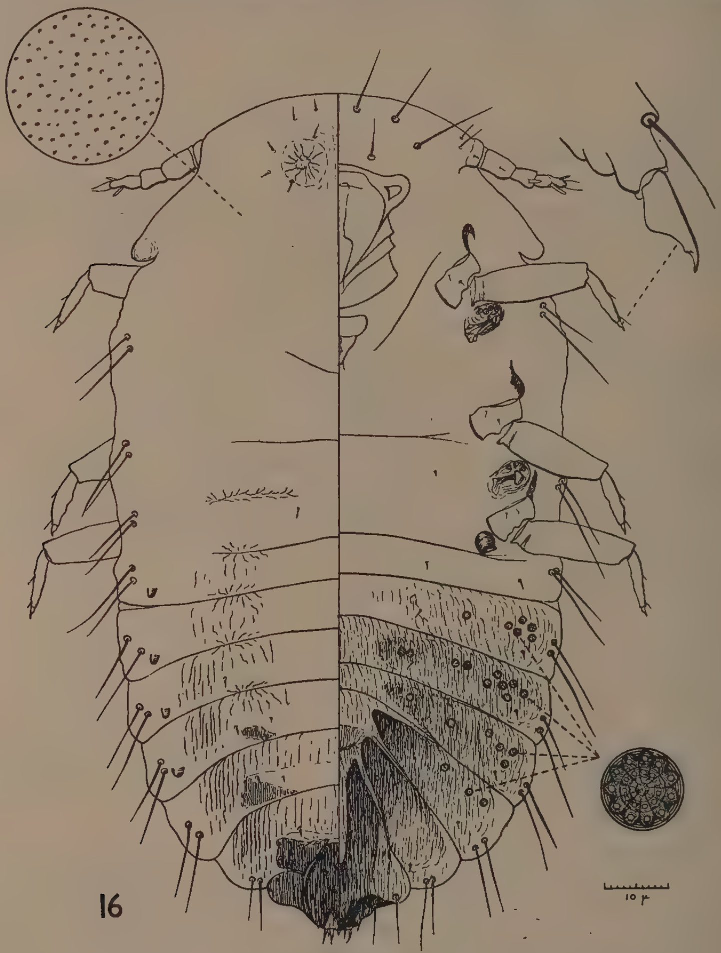

FIG. 16.—*Conchaspis newsteadi* Cockerell. Adult female.

Conchaspis orchidarum sp. n. (fig. 17).

Hosts and distribution.—Type and paratype from orchids, PANAMA: Canal Zone, at quarantine New York City (*H. B. Shaw*, No. 312) (letter dated 8.ix. 1916); other paratypes from *Lockhartia pallida*, PANAMA: Hoboken, Canal Zone, 16.iv.1941 (*Becker*, Hoboken No. 1190); from *Epidendrum ciliaris*

PANAMA: Hoboken, Canal Zone, 15.v.1946 (*Limber*, Hoboken, No. 6251); from *Oncidium ampliatum*, COLOMBIA: Carthagena, 4.v.1934 (*W. B. Wood*, No. B.P.O. A26163).

Habit.—Occurring on leaves of hosts.

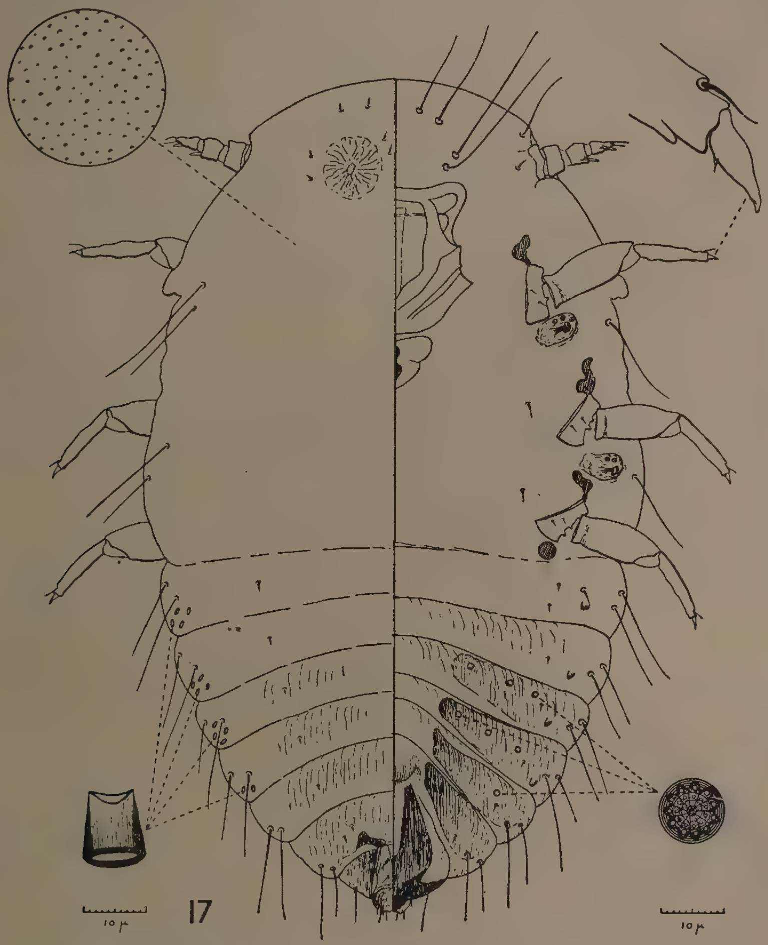

FIG. 17.—*Conchaspis orchidarum* Mamet, sp. n. Adult female.

Scale of female almost circular, white, semi-transparent, conical, with margin flattened, with 6 to 8 well-marked ridges or carinae radiating from the apex to the internal limit of the flattened margin. Diameter, about 2 mm.

Recognition characters.—Adult female elongate oval, prosoma very slightly swollen; derm membranous, very finely stippled. Antennae 4-segmented. Dorsal ocellar spots membranous, showing no trace of sclerotisation, with fine creases radiating from the central area. Length, about 2 mm.

Dorsal tubular ducts small, absent on metathorax, occurring on the first four abdominal segments marginally or submarginally in groups of 2–5, 3–5, 2–5 and 0–2 pores respectively. On the fourth segment, these ducts may not occasionally occur on one side but are always present on the other, so that it can be said that they are normally present on that segment.

Ventral multilocular pores occurring in a submarginal group, a submedian group and a group intermediate between the submedian and submarginal groups on the third and fourth segments of the abdomen and in only a submarginal group on the fifth segment; the submarginal groups of the third, fourth and fifth segments consisting of 1–2, 0–2, and 0–1 pores respectively; the intermediate groups of the third and fourth segments of 1 and 0–1 pore respectively, and the submedian groups of the third and fourth segments of 0–1 pore each.

Abdominal tubercles with smooth, rounded apices, occurring on first to fifth segments submarginally. Metathoracic dermal invaginations large, slightly sclerotised.

Notes.—This species is very closely related to *C. cordiae* Mamet, from which it can be separated by the characters given in the key to species which appears below. It is also readily distinguished from *C. angraeci* Cockerell, with which it has been confused, by the occurrence of dorsal tubular ducts on the first four abdominal segments submarginally.

The collections recorded by Swezey (1945, *Proc. Hawaii ent. Soc.* **12** : 374) under the name "*Conchaspis angraeci* Cockerell," as occurring on *Oncidium ampliatum*, from Colombia, and on *Lockhartia pallida*, from Canal Zone, Panama, are in reality referable to *C. orchidarum*. All the other records of this author are apparently referable to *C. angraeci*.

Specimens of this species were kindly made available by Dr. Harold Morrison.

Type and paratypes are in the collection of the United States National Museum, Washington, D.C.; other paratypes are in the author's collection.

Conchaspis pauliani Mamet (fig. 18).

1951, *Conchaspis pauliani* Mamet, *Mém. Inst. sci. Madagascar*, (A), **5** : 241.

Host and distribution.—Only known from the original record: On *Neodypsis ? articulatus*, MADAGASCAR: Tsaratanana Mt. (2000 m.).

Habit.—Occurring on leaves of host.

Scale of female circular, convex to more or less conical, pure white in colour, sometimes appearing dirty through accumulation of extraneous matter, somewhat shiny, showing circular ridges which give to it a roughened appearance. Central boss small, somewhat denser in texture than the rest of the scale, white, with eight carinae radiating from its centre to its margin.

Scale of male elongate, case-like, pure white in colour, smaller than that of female.

Recognition characters.—Adult female elongate, prosoma not swollen; derm slightly sclerotised especially at cephalic and posterior extremities; stippling not conspicuous. Antennae 4-segmented. Dorsal ocellar spots with strongly sclerotised anterior border, open posteriorly. Length, about 1 mm.

Dorsal tubular ducts small, occurring in marginal or submarginal groups on metathorax and first four abdominal segments, as follows: metathoracic group with 15–21 pores; groups of the first to fourth segments with 16–21, 14–16, 13 and 5–6 pores respectively.

Ventral multilocular pores entirely absent.

Metathoracic dermal invaginations fairly large and sclerotised.

Notes.—This species is related to *C. vayssierei* sp. n., from which it differs by the occurrence, on the abdominal segments, of tubular ducts of the small type only.

The above redescription and the accompanying figures are based upon specimens from the type material.

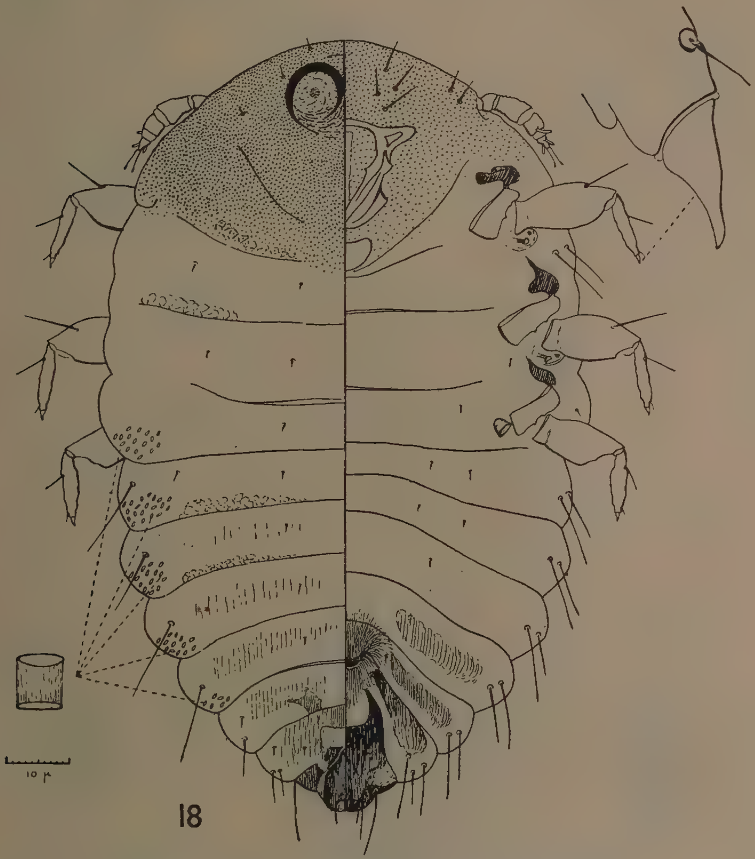

FIG. 18.—*Conchaspis pauliani* Mamet. Adult female.

Conchaspis phylicae sp. n. (fig. 19).

Host and distribution.—Type and paratype from *Phylica capitata*, SOUTH AFRICA : Cape of Good Hope, Stanford University Natural History Museum No. Herb. Spec. col. 1831, kindly made available by Prof. G. F. Ferris.

Habit.—Unknown.

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen ; derm fairly sclerotised, fairly coarsely stippled. Antennae 3-segmented.

Dorsal ocellar spots membranous, with a small, sclerotised central area. Length, about 1·4 mm.

Dorsal tubular ducts large, occurring in marginal or submarginal groups on metathorax and first four abdominal segments, as follows: metathoracic group with 2–3 pores; groups of first to fourth abdominal segments with 3–6, 3–4, 3–4, and 0–1 pores respectively.

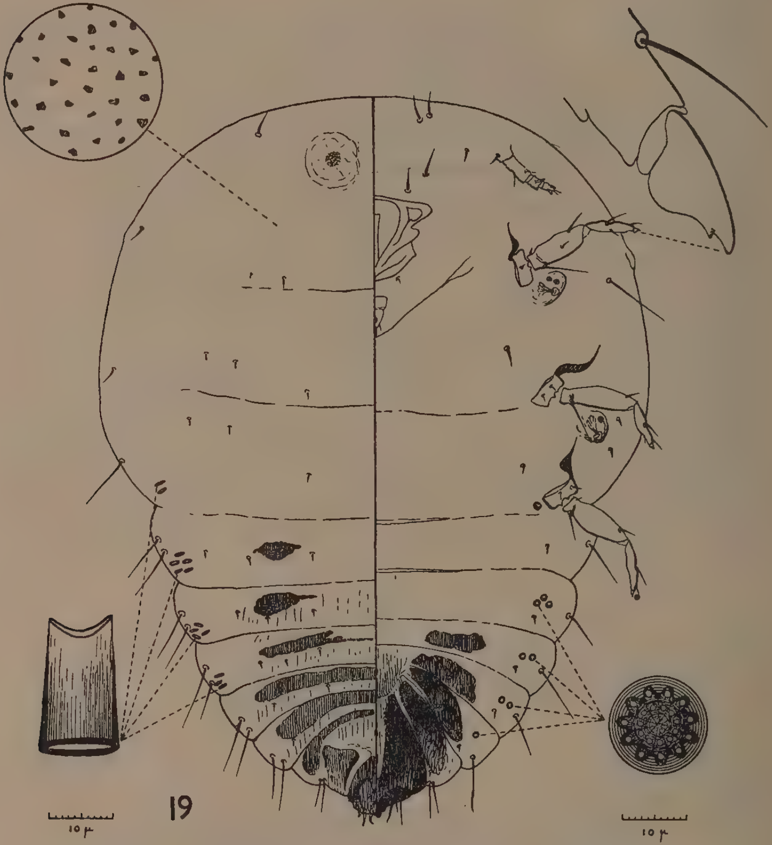

Fig. 19.—*Conchaspis phylicae* Mamet, sp. n. Adult female.

Ventral multilocular pores occurring submarginally on second to fifth abdominal segments in groups of 3–5, 2–3, 1–2, and 0–1 pores respectively.

Metathoracic dermal invaginations small, slightly sclerotised.

Notes.—The type has been deposited in the Stanford University Natural History Museum, California, U.S.A., and the paratype is in the author's collection.

Conchaspis socialis Green (fig. 20).

1896, *Conchaspis socialis* Green, *The Coccidae of Ceylon*, 1 : 20.
1903, *Conchaspis socialis* Green, Fernald, *Catalogue of the Coccidae of the World* : 39.
1921, *Conchaspis socialis* Green, MacGillivray, *The Coccidae* : 216.

Host and distribution.—Apparently known from the original record only : From an unidentified shrub, from Tangalla, Ceylon, John Pole collector.

Habit.—Occurring on twigs of host.

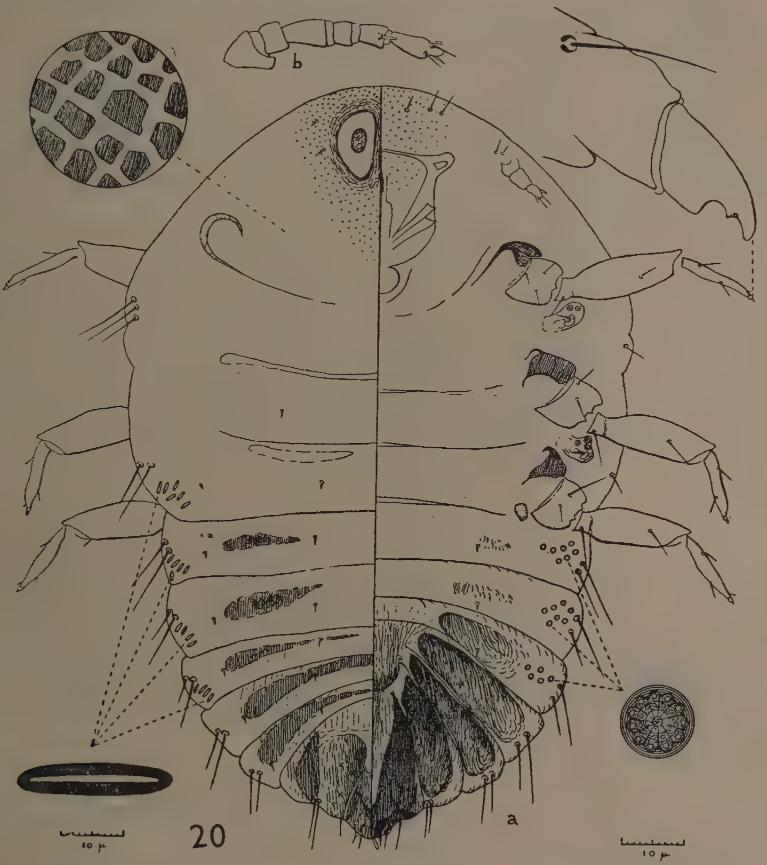

FIG. 20.—*Conchaspis socialis* Green. *a*, Adult female ; *b*, antenna of first stage larva.

Scale of female described by Green as “ . . . . comparatively large ; circular ; rounded to bluntly conical above ; firm, opaque and closely felted ; outer surface greyish to greyish brown ; inner surface white and smooth . . . Diameter of mature scale, about 5 mm.”

Scale of male described by Green as “ . . . white, oblong, flattened, closely felted, completely enveloping the pupa. The hinder extremity has a valvular opening. Length, 1·50 mm. Breadth, at widest part, about 0·75 mm." The male scales, according to Green, " . . . do not occur separately but are always collected together in groups of ten or more, beneath the parent scale which they completely fill."

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen; derm sclerotised, very coarsely stippled, shagreen-like. Antennae 3-segmented. Dorsal ocellar spots very conspicuous, represented as clear discs with sclerotised border and with central area sclerotised and circumscribed by a narrow but highly sclerotised rim. Length, about 1·3 mm.

Dorsal tubular ducts large, occurring in marginal or submarginal groups on metathorax and first four abdominal segments, as follows: metathoracic group with 4–6 pores; groups of first to fourth segments with 5–10, 4–8, 3–6 and 1–2 pores respectively.

Ventral multilocular pores occurring submarginally on first to third abdominal segments in groups of 3–8, 5–8, and 4–6 pores respectively.

Metathoracic dermal invaginations large, sclerotised.

First stage larva: Body elongate oval; derm fairly sclerotised, stippled. Antennae 6-segmented; third and sixth segments subequal and each nearly equal in length to the fourth and fifth together. Eyes submarginal. Dorsal ocellar spots conspicuous, represented as clear, roundish discs.

It has not been possible with the material at hand to ascertain whether dorsal tubular pores were occurring on the abdominal segments marginally. Length 0·3 mm.

Notes.—*C. socialis* Green is related to *C. lata* Hempel, from which it can be separated by the structure of the ocellar spots, the stippling of the derm, the size of the dorsal tubular ducts, and the constant absence of ventral multilocular pores on the fourth abdominal segment submarginally.

The above redescription and the accompanying figures are based upon specimens from the type material which has been made available by Mr. J. P. Doncaster, of the British Museum.

Conchaspis tsaratananae Mamet (fig. 21).

1951, *Conchaspis tsaratananae* Mamet, *Mém. Inst. sci. Madagascar* (A), **5**: 243.

Hosts and distribution.—Originally described as from an undetermined species of palm, MADAGASCAR: Tsaratanana Mt. (2000 m.) No. 125. Other collections, from *Neodypsis* sp., from Antsily near Sandrakely, Madagascar, ii.1950, R. Paulian collector, No. 333, and from a palm, Tsaratanana Mt. (2000 m.), Madagascar, ii.1950, R. Paulian collector, have kindly been made available by the collector.

Habit.—Occurring on the lower surface of leaves of hosts.

Scale of female somewhat elongate oval, very thin, delicate, more or less translucent, white to dirty-white, flat. Central boss small, somewhat denser in texture than surrounding structures, white, with slightly elevated carinae radiating from its centre.

Scale of male, opaque, dirty-white, smaller than that of female.

Recognition characters.—Adult female elongate, with prosoma not swollen; derm slightly sclerotised especially at the anterior and posterior extremities, with stippling not conspicuous. Antennae 4-segmented. Dorsal ocellar spots fairly large, completely circumscribed by a sclerotised border. Length, about 0·6 mm.

Dorsal tubular ducts large, occurring marginally or submarginally on first to fourth abdominal segments in groups of 1–3, 1–2, 1–2 and 1 pores respectively. One duct very occasionally occurring on metathorax submarginally.

Ventral multilocular pores occurring singly on third to sixth abdominal segments submarginally.

Metathoracic dermal invaginations large, somewhat sclerotised.

Notes.—The above redescription and the accompanying figure are based upon specimens from the type material.

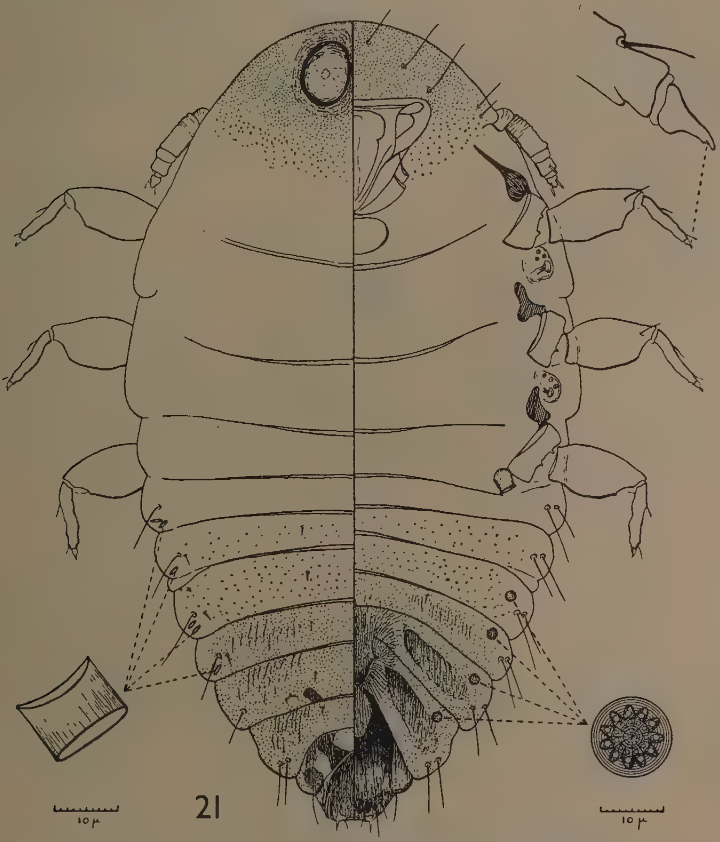

FIG. 21.—*Conchaspis tsaratananae* Mamet. Adult female.

Conchaspis tsinjoarivensis sp. n. (fig. 22).

Host and distribution.—Type and paratypes from an undetermined shrub, MADAGASCAR : Tsinjoarivo, 25.v.1950 (*R. Paulian* and *Ray. Mamet*, No. 230).

Habit.—Occurring on stems and twigs of host.

Scale of female circular to oval, moderately convex, of somewhat hard texture, white, somewhat obscured by particles of extraneous matter, without conspicuous ridges, occurring singly or in compact masses; central boss fairly conspicuous, somewhat shiny. Internally, the scale is pure white and nacreous. Diameter, about 4 mm.

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen; derm sclerotised, shagreen-like. Antennae 2-segmented. Dorsal ocellar spots relatively small, represented as clear discs with central area sclerotised and circumscribed by a narrow highly sclerotised border. Length, about 0·8 mm.

Dorsal tubular ducts large, occurring in marginal or submarginal groups on metathorax and first five abdominal segments, as follows: metathoracic group with 1–4 pores; groups of first to fifth abdominal segments with 4–8, 2–7, 1–3, and 0–1 pores respectively.

Ventral multilocular pores always occurring singly on second to fourth abdominal segments submarginally.

Metathoracic dermal invaginations large, somewhat sclerotised.

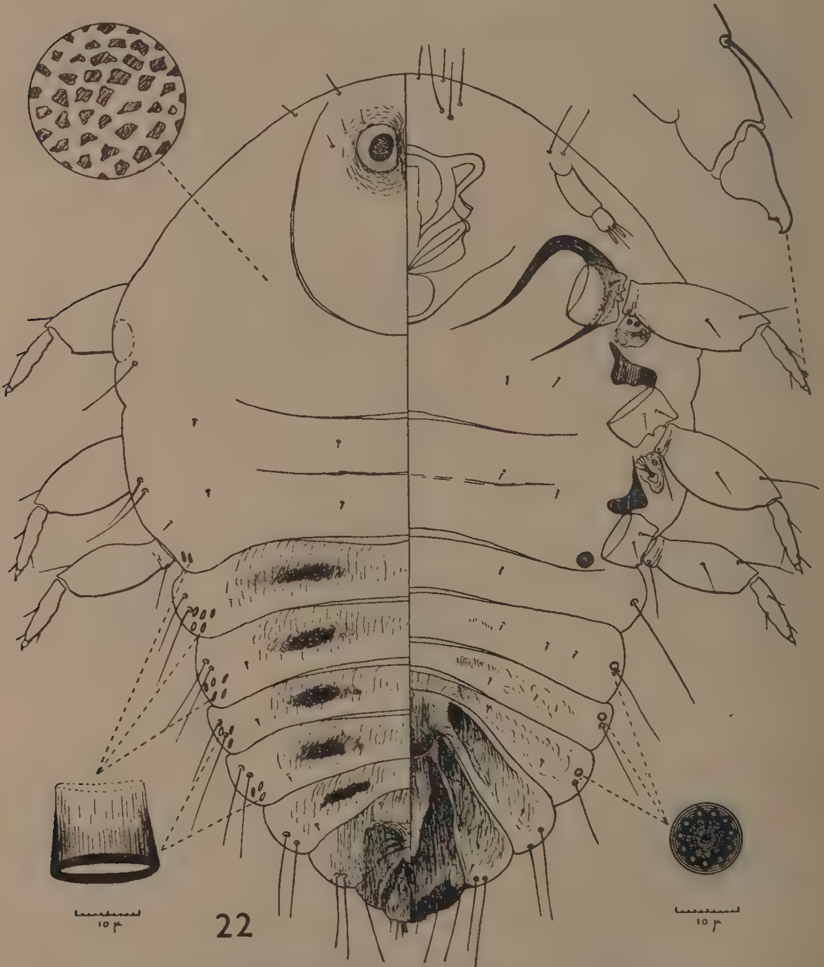

Fig. 22.—*Conchaspis tsinjoarivensis* Mamet, sp. n. Adult female.

Notes.—This species is very near to *C. vaughani* sp. n. from which it differs by the complex of characters given in the key to species of the genus.

The type and a paratype are in the author's collection. Other paratypes have been deposited in the collection of the Institut de Recherche Scientifique de Madagascar, the British Museum and the United States National Museum.

Conchaspis vaughani sp. n. (fig. 23).

Host and distribution.—Type and paratypes from an undetermined tree, from MADAGASCAR : Manjakatompo, 24.v.1950 (*R. Paulian* and *Ray. Mamet*,

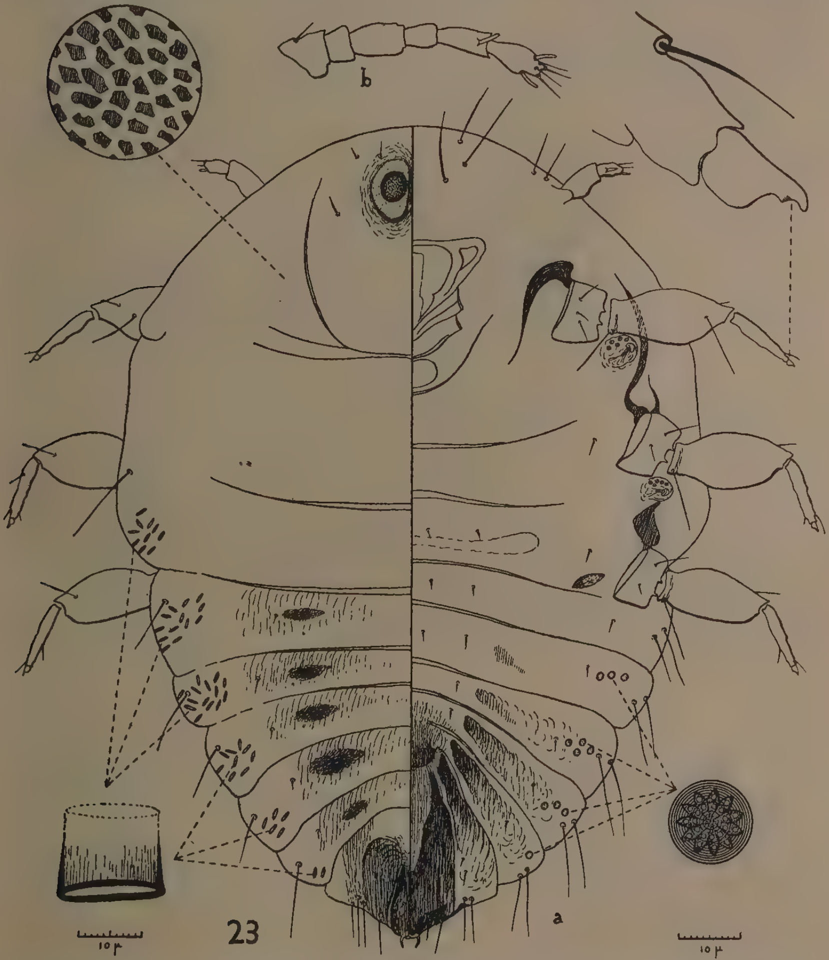

FIG. 23.—*Conchaspis vaughani* Mamet, sp. n. *a*, Adult female ; *b*, antenna of first stage larva.

No. 219); other paratypes from an undetermined shrub, same locality, 24.v.1950 (*Ray. Mamet*, No. 220).

Habit.—Occurring on upper and lower surfaces of leaves and on twigs of hosts.

Scale of female almost circular, moderately convex, of somewhat hard texture, white, usually obscured by extraneous matter, without conspicuous ridges, usually occurring singly on leaves and in small masses on twigs; central boss not conspicuous. Internally the scale is pure white and nacreous. Diameter, about 4 mm.

Scale of male elongate, white and shiny; occurring in radially disposed elements under female scale, with posterior extremity protruding beyond margin of female scale.

Recognition characters.—Adult female of the shape common to the genus, with prosoma swollen; derm sclerotised, very coarsely stippled to shagreen-like. Antennae 2-segmented. Dorsal ocellar spots represented as clear discs with central area sclerotised and circumscribed by a narrow, highly sclerotised border. Length, about 0·8 mm.

Dorsal tubular ducts large, occurring in marginal or submarginal groups on metathorax and first five abdominal segments, as follows: metathoracic group with 5–10 pores; groups of first to fifth abdominal segments with 10–13, 8–14, 5–12, 2–7 and 1–2 pores respectively.

Ventral multilocular pores occurring submarginally on second to fifth abdominal segments in groups of 1–4, 1–4, 1–3 and 0–1 pores respectively.

Metathoracic dermal invaginations large, somewhat sclerotised.

First stage larva: Body elongate oval; derm fairly sclerotised, stippled. Antennae 6-segmented; third, fifth and sixth segments subequal. Eyes submarginal. Dorsal ocellar spots conspicuous, represented as clear discs. Dorsal tubular pores large, occurring singly on each of the first, second and third abdominal segments submarginally. Length, about 0·3 mm.

Notes.—This species is very near to *C. tsinjoarivensis* Mamet from which it is distinguished by the more numerous dorsal tubular ducts and ventral multilocular pores.

The type and paratypes are in the author's collection. Other paratypes have been deposited in the collection of the British Museum, the United States National Museum, the Muséum National d'Histoire Naturelle de Paris, the Institut de Recherche Scientifique de Madagascar, and in the Stanford University Natural History Museum, California, U.S.A.

This species is named in honour of the distinguished botanist, Dr. R. E. Vaughan, Director of the Mauritius Institute.

Conchaspis vayssierei sp. n. (fig. 24).

Hosts and distribution.—Type and paratype from *Areca* sp., MADAGASCAR, v.1935 (*L. P. Regnard*). Other paratypes from an undetermined species of palm, MADAGASCAR, 1921 (*G. Petit*), from an undetermined palm, MADAGASCAR: Soalala, Mitsinjo region, 4.ix.1952 (*R. Paulian*).

Other collections from *Oreodoxa regia*, MADAGASCAR: Ambanja, 25.xi.1952 (*E. S. Brown*) (per Commonwealth Institute of Entomology); from *Cocos nucifera*, MADAGASCAR: Nossi-bé Island, iv.1953 (*R. Paulian*).

Habit.—Occurring on upper and lower surfaces of leaves of hosts.

Scale of female circular, white, somewhat shiny, closely felted in texture; semi-transparent, moderately convex; occurring singly or grouped together; central boss conical, opaque, white, with numerous ridges radiating from its apex to its margin. Diameter, about 2·5 mm.

Scale of male elongate, white, felted in texture, semi-transparent, somewhat shiny, with boss opaque.

Recognition characters.—Adult female more or less elongate, with prosoma a little swollen; derm slightly sclerotised, with stippling not conspicuous. Antennae 4-segmented. Dorsal ocellar spots with a strongly sclerotised and thick anterior border, open posteriorly. Length, about 0·6 mm.

Dorsal tubular ducts of the small and large types: ducts of the small type occurring in marginal or submarginal groups of 4–7 each on metathorax and first abdominal segment; those of the large type occurring marginally or submarginally on second to fourth abdominal segments in groups of 2–6, 2–5 and 2–3 pores respectively.

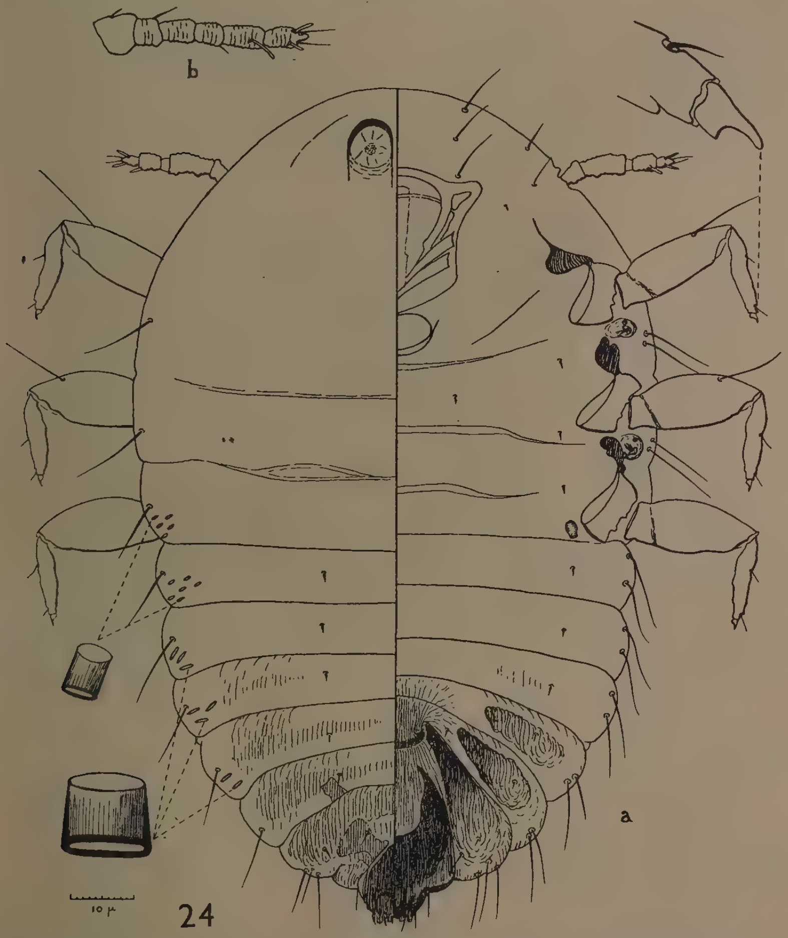

FIG. 24.—*Conchaspis vayssierei* Mamet, sp. n. *a*, Adult female ; *b*, antenna of first stage larva.

Ventral multilocular pores absent.

Metathoracic dermal invaginations small, slightly sclerotised.

First stage larva: Body elongate oval; derm slightly sclerotised, finely stippled. Antennae 6-segmented; fifth and sixth segments subequal. Eyes marginal. Dorsal ocellar spots fairly conspicuous, represented as clear roundish discs with a few creases. Dorsal tubular pores large, occurring singly on the margin of each of the second and third abdominal segments. Length, 0·3 mm.

Notes.—This is the only known species of *Conchaspis* in which tubular ducts of both the small and large types occur.

The type and a paratype have been deposited in the collection of the British Museum. Other paratypes are in the collection of the United States National Museum, the Muséum National d'Histoire Naturelle de Paris, the Stanford University Natural History Museum, the Institut de Recherche Scientifique de Madagascar and in that of the author.

This species is named after Prof. Paul Vayssière, who very kindly made available to the author the numerous specimens of this species collected by G. Petit in 1921.

VII. Key to Adult Females of Species of the Genus *Conchaspis*.

1. Antennae 5-segmented . . . . **fluminensis** Hempel.
   Antennae with less than 5 segments . . . . 2.
2. With only the metathoracic pair of ventral dermal invaginations present 3.
   With a metathoracic and a mesothoracic pair of ventral dermal invaginations present . . . . **madagascariensis** sp. n.
3. Ventral multilocular pores occurring on the prosoma submarginally **insolitus** sp. n.
   Not so . . . . 4.
4. Tubular ducts always absent on metathorax and on abdominal segments . . . . 5.
   Tubular ducts always present on metathorax and/or on abdominal segments . . . . 6.
5. A submarginal group of 1–5 multilocular pores always occurring on the second abdominal segment ventrally; intermediate group of same segment always with 1–2 similar pores . . **newsteadi** Cockerell.
   Only one multilocular pore very occasionally occurring on the second abdominal segment submarginally and in the intermediate position **angraeci** Cockerell.
6. Multilocular pores entirely absent . . . . 7.
   Multilocular pores present on the abdominal segments only . . . 9.
7. Prosoma swollen; ocellar spots represented by clear discs with sclerotised central area; antennae 3-segmented . . . . **euphorbiae** Brain.
   Prosoma not swollen; ocellar spots with strongly sclerotised border which is open posteriorly; antennae 4-segmented . . . . . 8.
8. Only tubular ducts of the small type present on abdominal segments; number of such ducts in first abdominal group always exceeding 15 **pauliani** Mamet.
   Tubular ducts of both the small and large types present on abdominal segments; number of ducts in first abdominal group never exceeding 7 . . . . **vayssierei** sp. n.

9. Multilocular pores occurring in submarginal, submedian and intermediate groups on third and fourth abdominal segments . . . . 10.
Multilocular pores occurring in submarginal groups only . . . . . 11.

10. Tubular ducts usually present on fourth abdominal segment submarginally and always absent on metathorax ; scale of female with 6–8 conspicuous ridges radiating from central apical area ; on orchids . . . . **orchidarum** sp. n.
Tubular ducts always absent on fourth abdominal segment submarginally and present on metathorax ; scale of female without conspicuous ridges radiating from central apical area ; not on orchids **cordiae** sp. n.

11. Multilocular pores always absent on first abdominal segment . . . 12.
Not so . . . . 15.

12. Ocellar spots showing some sort of sclerotisation . . . . 13.
Not so . . . . 14.

13. Prosoma swollen ; multilocular pores present on second abdominal segment ; antennae 3-segmented . . . . **phylicae** sp. n.
Not so ; antennae 4-segmented . . . . **tsaratananae** Mamet.

14. Tubular ducts present on metathorax submarginally **diplothemii** Lepage and Giannotti.
Not so . . . . **lepagei** Hempel.

15. Antennae 2-segmented . . . . 16.
Antennae 3-segmented . . . . 17.

16. Number of tubular ducts in each metathoracic group always exceeding 5 ; first abdominal segment with a marginal or submarginal group of 10 tubular ducts or more ; second abdominal segment usually with more than one multilocular pore submarginally ; fifth abdominal segment usually with one multilocular pore submarginally **vaughani** sp. n.
Metathorax never with more than 4 ducts submarginally ; first abdominal segment never with more than 8 ducts marginally or submarginally ; multilocular pores on second abdominal segment always occurring singly ; multilocular pores always absent on fifth abdominal segment submarginally . . . . . . **tsinjoarivensis** sp. n.

17. Ocellar spots with anteriorly open sclerotised border ; multilocular pores in groups never exceeding 4 in number and generally occurring on the fourth abdominal segment submarginally . . . . **lata** Hempel.
Ocellar spots represented as clear discs with sclerotised central area circumscribed by a narrow, highly sclerotised rim ; multilocular pores in groups always exceeding 4 in number and always absent on fourth abdominal segment . . . . **socialis** Green.

Vol. 105. Part 12. Pp. 241–268. 90 figs. 15th July, 1954

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THE EPHEMEROPTERA OF EASTERN AUSTRALIA.

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Manuscript received 1st October, 1953.
(Read 4th November, 1953.)

With 90 Text-figures.

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1. Introduction.

The Australian mayflies are a still practically undescribed fauna. In a previous paper (Harker, 1950) a few of the commoner species were described, but the region in which collections were made was limited, and it was difficult to time collections over the distances involved during the brief season in which subimagines emerged, so that the number of specimens available was small. Since the author avoided describing species when less than a series of twenty specimens had been examined, a number of new species was at that time recognised but not described. Now, owing to the generosity of Mr. D. E. Kimmins of the British Museum (Natural History), the Tillyard Collection has been made available, and these specimens, together with those previously collected, have enabled a number of new species to be distinguished.

My sincere thanks go to Mr. Kimmins for his assistance, and to Mr. B. McMillan who collected so many of the specimens in my original series.

Methods.

Measurements : All measurements have been made from a series of a minimum of twenty specimens, unless otherwise stated. The measurement given is the average of these figures, the range of the measurements appears in brackets. The body-length has been taken in the penultimate instar nymph from the anterior edge of the clypeus to the base of the caudal filaments. Unless otherwise stated, specimens examined have been collected by the author.

Wings: Where the cross venation varies throughout the series the text figure shows the maximum number. Text-figures have been drawn with the aid of a micro-projector, or, in the case of genitalia, with a camera lucida.

2. LEPTOPHLEBIIDAE.

KEY TO GENERA.

Imagines.

1.	Tarsal claws of each pair similar	2.
	Tarsal claws of each pair dissimilar	4.
2.	In the hind wing Sc reaches wing margin at nine-tenths of wing length	3.
	In the hind wing Sc reaches wing margin at three-quarters of wing length	**Atalonella** Needham and Murphy
3.	In the hind wing cross veins may be present in anal region. Basal segment of forceps in male narrows abruptly	**Atalophlebia** Eaton
	No cross veins present in the anal region of hind wing. Basal segment of forceps narrows gradually	**Atalomicria** gen. n.
4.	Fore wing two or three times as long as broad	5.
	Fore wing five times as long as broad	**Jappa** gen. n.
5.	Sc of the hind wing runs parallel to R_1 at wing tip. The intercalary of CuA in fore wing arises midway between CuA and CuP	**Kirrara** gen. n.
	Sc of the hind wing turns down towards R_1 at wing tip. The intercalary of CuA arises from, or close to, CuA_1	**Deleatidium** Eaton.

Nymphs.

1.	Gills lanceolate	2.
	Gills broad, undivided or divided	4.
2.	Gills single	**Deleatidium**
	Gills double	3.
3.	First segment of maxillary palp very short	**Deleatidium** (**Atalophlebiodes**)
	First segment of maxillary palp long, about equal to second and third together	**Atalonella**
4.	Two tusk-like projections arising from front of head	**Jappa**
	No such projections	**Atalophlebia**

Atalonella Needham and Murphy, 1924.

KEY TO SPECIES.

1.	Two halves of penis distinctly separated forming a V shape	3.
	Two halves of penis only slightly divided	2.
2.	Forceps base straight	**A. parva** (Harker)
	Forceps base concave	**A. simillima** (Ulmer)
3.	Penis with two small acute projections on adjacent surfaces of the two halves	**A. fuscula** (Tillyard)
	Not so	4.

4. Penis with three terminal rounded embossments . **A. delicatula** (Tillyard)
Penis with simple rounded tip . . . . . 5.
5. Lateral edges of penis bearing a rounded projection . . **A. lucida** (Ulmer)
Lateral edges of penis concave . . . . . **A. brunnea** (Tillyard)

The genus *Atalonella* has been questioned by several authors (Lestage, 1931; Ulmer, 1938; Traver, 1946; Harker, 1950). No type-species was designated by Needham and Murphy, but the species described at the same time, *Atalonella ophis*, was probably considered as such.

Needham and Murphy distinguished *Atalonella* from *Atalophlebia* by a number of characteristics which they found separated *Atalonella ophis* from a species which they described as *Atalophlebia fulvipes*, which latter has since been transferred to *Atalophlebiodes* (Ulmer, 1938). That is, they did not compare the type species *Atalonella ophis* and *Atalophlebia australis*, and when these two are compared it is, in fact, found that the characters on which Needham and Murphy separated the two genera are not distinct in the majority of cases. However, although the distinction between the two genera is not valid for these characters, there is little doubt that *Atalonella ophis* does belong to a different genus from *Atalophlebia australis*, and can be distinguished from it by the following characters:

Imago: In the fore wing CuP is straight in its basal portion, and does not curve upwards acutely towards CuA, as it does in *Atalophlebia*. The veins in the basal half of the costal area are weak or absent. In the hind wing the costal border is angulated and bends down sharply to meet Sc before that vein reaches the wing tip. There is no intercalary present in the fork of MP, as is present in *Atalophlebia*; there are no cross veins posterior to CuA.

Nymph: The gills are lanceolate, otherwise the nymphs are very similar to those of *Atalophlebia*.

It has been found that, once this distinction has been made between the two genera, several species previously described in *Atalophlebia* must be transferred to *Atalonella*. They are as follows:

Atalonella parva (Harker, 1950) **comb. nov.** It should be noted that the figure of the fore wing in this species in the original description should show CuA straight and not curved.

Atalonella brunnea (Tillyard, 1933) **comb. nov.**

Atalonella fuscula (Tillyard, 1933) **comb. nov.**

Atalonella delicatula (Tillyard, 1933) **comb. nov.**

Specimens of *Atalophlebia simillima* Ulmer, and *Atalophlebia lucida* Ulmer have not been seen, but from the figures accompanying their descriptions (Ulmer, 1919) they also seem to belong to *Atalonella*. *A. fusca* (Ulmer) has previously been moved to *Atalonella* by Needham and Murphy.

It is interesting to note that Tillyard (1935) remarked on the two quite distinct groups formed by the Tasmanian species he described in *Atalophlebia*; it is one of these groups which, in this paper, is moved to *Atalonella*.

Atalophlebia Eaton, 1881.

KEY TO IMAGINES.

1. Rs arises in basal half of hind wing and is connected by a cross vein at its origin to R_1 . . . . . 2.
Rs arises half-way between base and apex of hind wing, or in apical half of wing, not connected to R_1 at its origin . . . . . 7.

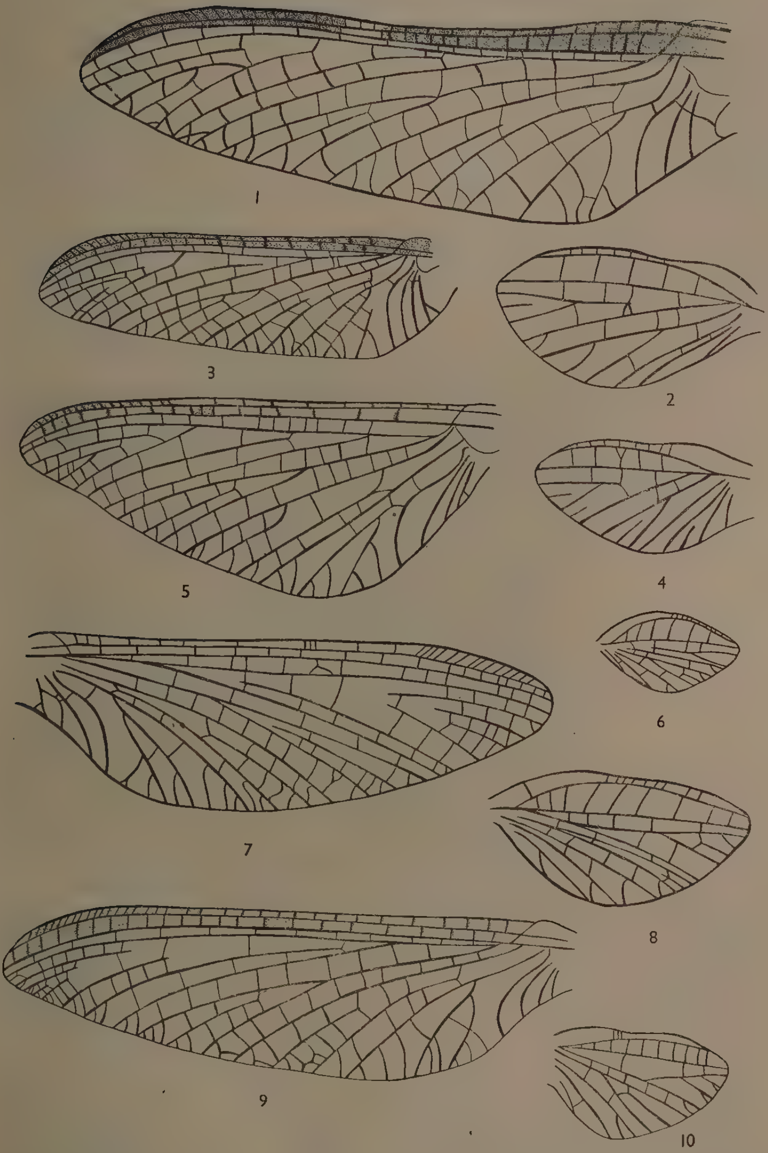
2. Fore wing shaded in at least some region of C and Sc areas . . . 3.
Fore wing not so shaded . . . . **A. kala** sp. n.
3. Forked cross veins present in pterostigmatic area of fore wing . . . 4.
No such forked cross veins . . . . 5.
4. Appendix dorsalis present . . . . **A. longicaudata** Harker.
Appendix dorsalis absent . . . . **A. superba** Tillyard.
5. Cross veins absent in cubital and anal areas of hind wing . **A. ida** Tillyard
Cross veins present in cubital and anal areas of hind wing . . . . 6.
6. No cross veins present in basal half of costal area of hind wing
A. kokunia sp. n.
Cross veins present in basal half of costal area of hind wing
A. maculosa Harker
7. Penis not reaching beyond narrowing of first segment of forceps . . 8.
Penis reaching beyond narrowing of first segment of forceps . . . 11.
8 Forceps base convex . . . . **A. hudsoni** Tillyard
Forceps base not convex . . . . 9.
9. Appendix dorsalis present . . . . 10.
Appendix dorsalis absent . . . . **A. albiterminata** Tillyard
10. The C and Sc areas of forewing shaded right to wing base . **A. tuhla** sp. n.
Fore wing not so shaded . . . . **A. australis** (Walker)
11. Penis long and thin . . . . **A. pierda** sp. n.
Penis about as wide as it is long . . . . 12.
12. Penis with pointed tip . . . . **A. australasica** Pictet
Not so . . . . 13.
13. Tips of the two halves of penis directed away from each other . . . 14.
Tips of the two halves of penis parallel. . . . . . . **A. incerta** Harker
14. Penis with two spines at tip of each half . . . . **A. marowana** Harker
No such spines . . . . **A. miunga** sp. n.

The most commonly occurring genus in Eastern Australia is *Atalophlebia*. This genus was first described by Eaton in 1881, with *A. australis* (Walk.) designated as the type-species. In his second monograph on the Ephemeroptera, Eaton placed fifteen species in this genus, six of them being from Australia. In 1916 and 1919 Ulmer described a further five species from Queensland. Tillyard described six species from Tasmania in 1935, three of which are transferred to the genus *Atalonella* in the present paper. In 1950 the author described five species from New South Wales, one of which is now moved to *Atalonella*.

The nymphs of some of these species have now been discovered, and their descriptions follow, together with those of five new species.

Atalophlebia kokunia sp. n.

Male Imago.—Measurements : Fore wing 9 mm. (7–10 mm.). Hind wing 3 mm. *General colour :* Yellowish brown with brown markings. *Wings :* Veins brown. In the fore wing (fig. 5) cross veins in costal and subcostal areas shaded with brown, and in pterostigmatal area membrane also shaded brown. Just below the bulla is one brown patch in subcostal area. Hind wing (fig. 6) with a very narrow costal area with a few cross veins. Rs arises close to wing base, and fork of MP at about half distance from base to apex. *Legs :* Yellowish with two dark bands on femur and one on tarsus. In the fore leg tarsus slightly longer than tibia, which is again longer than femur ; tarsal segments in descending order of length are 2 = 3, 4, 5, 1 (fused with tibia). The hind



Figs. 1–10.—Imaginal wings. *Atalophlebia tuhla* sp. n. (1) Fore wing. (2) Hind wing. *Atalophlebia australasica* (Pict.). (3) Fore wing. (4) Hind wing. *Atalophlebia kokunia* sp. n. (5) Fore wing. (6) Hind wing. *Atalophlebia kala* sp. n. (7) Fore wing. (8) Hind wing. *Atalophlebia miunga* sp. n. (9) Fore wing. (10) Hind wing.

leg is missing in the holotype. Order of tarsal segments of middle leg is 5, 2, 3, 4, 1 (fused with tibia). Both tarsal claws of each pair alike and acute. *Genitalia :* Missing.

Subimago.—Cross veins irregularly shaded with brown, giving a distinctive pattern to wings (fig. 13).

Female imago, nymph.—Unknown.

Holotype male, QUEENSLAND : Eidswold, 28.viii.1929. Morphotype subimago : QUEENSLAND : Eidswold, 19.ix.1929 (*R. J. Tillyard*). In British Museum (Natural History). All types pinned and set. Only four specimens of this species have been examined.

Atalophlebia miunga sp. n.

Male imago.—Measurements : Fore wing 9 mm. (8·0–10 mm.). Hind wing 2 mm. *General colour :* Light brown with darker head and thorax. *Wings :* Veins dark brown. In the fore wing (fig. 9) cross veins in basal half of subcostal area heavily shaded. Pterostigmatic area opaque and cross veins in the region are not shaded. Cross veins in costal area of pterostigmatic area forked. Costal space of hind wing (fig. 10) long and very narrow, with a number of cross veins. Rs arises in apical half of wing, and MA is forked basally to this. *Genitalia* (fig. 35) : Light brown. Penis somewhat similar to that of *A. incerta*, but tips of the two halves point away from each other, whereas they are parallel in *A. incerta*. Appendix dorsalis well developed, no banding present on cerci.

Female imago, subimago, nymph.—Unknown.

Holotype male, NEW SOUTH WALES : Armidale, 3000 ft., xi.1948. In British Museum (Natural History). In alcohol, genitalia dissected, and mounted on a separate slide. Only five specimens of this species have been examined.

Atalophlebia pierda sp. n.

Male imago.—Measurements : Fore wing 11 mm. (10·5–12 mm.). Hind wing 4 mm. *General colour :* Brown with dark brown markings. *Wings :* Veins brown. In the fore wing (fig. 11) costal and subcostal area yellowish-brown, and cross veins shaded dark brown. Pterostigmatal area slightly darker with one dark patch in subcostal area below bulla. Costal space in hind wing (fig. 12) long and narrow, with a number of cross veins. Rs arises in this wing at about two-thirds of distance from base to apex, and fork of MP is slightly basal to this. *Legs :* Reddish-brown with two dark bands on femur and one on tibia. Tarsus of fore leg longer than tibia, which is again longer than femur. Tarsal segments in descending order of length are 2, 3 = 4, 5, 1 (fused with tibia). In middle and hind legs order of tarsal segments is 5, 2 = 3, 4, 1 (fused with tibia). Tarsal claws all alike and acute. *Genitalia* (fig. 37) : Forceps light brown, penis darker. Penis long and extending well beyond the narrowing of first segment of forceps. Cerci brown, with slightly darker brown bands. Appendix dorsalis well developed.

Female imago.—Subanal plate bears a deep semicircular incision.

Subimago.—Wings brown, with all cross veins very slightly shaded, the imaginal colouring showing through in costal and subcostal area of fore wing.

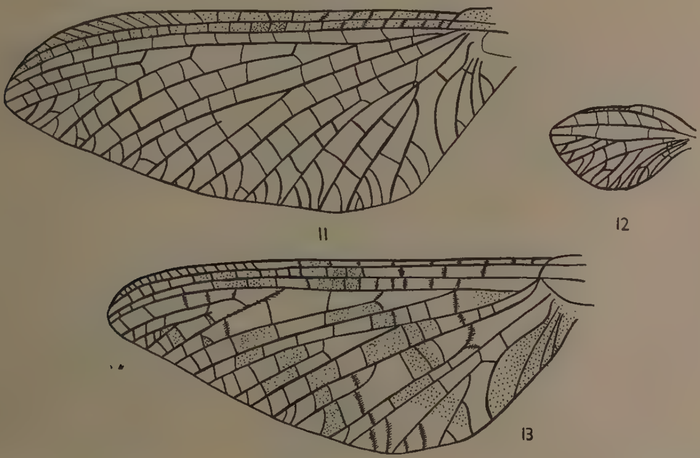
Holotype male, NEW SOUTH WALES : Hornsby, 21.ix.1917. Allotype female, N.S.W. : Hornsby, 22.ix.1917. Morphotype subimago and paratypes, N.S.W. : Hornsby, 24.ix.1917 (*R. J. Tillyard*). In British Museum (Natural History). All types pinned and set. Specimens examined from N.S.W. : Epping, xii.1948.

This species superficially resembles the New Zealand species, *A. dentata* (Eat.), but differs from it in the form of the genitalia.

Atalophlebia tuhla sp. n.

Male imago.—Measurements : Fore wing 12 mm. (10–14 mm.). Hind wing 3 mm. *General colour :* Yellow brown with dark brown markings. *Wings :* Veins dark brown. In fore wing (fig. 1) costal and subcostal area uniformly dark brown except for one clear patch near the bulla. Base of wing clouded with brown. Length from base to tornus short. Hind wing (fig. 2) about two-thirds as wide as long. Costal space long and very narrow, and a number of cross veins present. MP forked at slightly less than half distance from base to apex. *Legs :* Yellow brown, with two black bands on femur. Tibia longer than femur in fore legs, and tarsus longer again. Tarsal segments in descending order of length are 2, 3, 4, 5, 1 (fused with tibia). Tarsal claws all acute. *Genitalia :* (fig. 34) Forceps very long, and first segment broad for about two-thirds of its length. Penis large, but does not protrude as far as the narrowing of first segment of forceps. Appendix dorsalis well developed.

Female, subimago, nymph.—Unknown.



FIGS. 11–13.—*Atalophlebia pierda* sp. n. (11) Fore wing. (12) Hind wing. (13) Fore wing of subimago of *Atalophlebia kokunia* sp. n.

Holotype male, NEW SOUTH WALES : Kiandra, 15.i.1930 (*R. J. Tillyard*). In British Museum (Natural History). Pinned and set. Genitalia dissected off, and mounted on a separate slide. Paratypes. N.S.W. : Armidale, Commissioners Waters, 3000 ft., iv.1948.

Atalophlebia kala sp. n.

Male imago.—Measurements : Fore wing 12 mm. (11–13). Hind wing 3 mm. *General colour :* Light brown. *Wings :* Veins light brown. In fore wing (fig. 7) costal and subcostal areas unshaded. Cross veins in pterostigmatic area slanting and slightly forked. Costal space in hind wing (fig. 8) long and narrow with a number of cross veins. Rs arises at about one-third of distance from base to apex, and fork of MP is considerably basal to this. *Legs :* Darker than body, with a faint indication of two darker bands on femur. Tarsus of fore legs missing on specimens examined, tibia nearly twice as long as femur. In hind legs tibia longer than femur, tarsus being very short. Tarsal segments in descending order of length are 5, 4 = 3 = 2, 1 (fused with tibia). Tarsal claws all acute. *Genitalia* (fig. 36): Forceps light brown, penis darker. Penis short, not reaching the narrowing of first segment of forceps. Cerci brown with slightly darker annulations. Appendix dorsalis well developed.

Female imago.—Subanal plate bears a deep V-shaped incision.

Subimago.—All cross veins very slightly shaded with brown, giving the wing a slightly darker appearance than that of imago.

Holotype male, NEW SOUTH WALES: Mt. Kosciusko, Lake Albina, 2.ii.1929 (*R. J. Tillyard*). Allotype female, morphotype subimago and paratypes, N.S.W.: Mt. Kosciusko, Lake Cootapatamba 6600 ft., 27.i.1930 (*R. J. Tillyard*). In British Museum (Natural History). All types pinned and set. Genitalia dissected and mounted on separate slide.

Atalophlebia australasica (Pictet).

A. australasica has been placed previously in synonymy with *A. costalis* (Burmeister) by Ulmer (1919). In the British Museum there are specimens of *A. australasica* determined by Eaton which fit the original description given by Pictet, and which are very similar to the coloured plate given in his paper. Specimens of *A. costalis* determined by Tillyard, and also fitting the original description of Burmeister and Eaton's later brief description, show that these two are quite distinct species.

Mr. D. E. Kimmins has drawn my attention to the preoccupation of *A. costalis*, originally described in *Baetis*, by *Baetis costalis* Curtis, 1834 (now a synonym of *Heptagenia sulphurea*). In the British Museum there are specimens of *A. albiterminata* Tillyard, the type of which is missing, determined by Tillyard, and these are indistinguishable from those also determined by him as *A. costalis*. In the original description Tillyard refers to the close similarity of the two species, but does not differentiate between them, and since his two series are so very similar *A. albiterminata* is now thought to be in synonomy with *A. costalis*. As *A. costalis* is preoccupied, it should take the name of its first synonym and be known as *A. albiterminata*.

As no very full description of *A. australasica* is known to exist, the following features are thought to be worth recording.

Male imago.—*Measurements:* Fore wing 10 mm. (9–11 mm.). Hind wing 2 mm. *General colour:* Brown with light brown markings. *Wings:* Veins dark brown. In the fore wing (fig. 3) whole of costal and subcostal area dark yellow, and all cross veins in this area shaded with dark brown. Pterostigmatal region slightly darker than the more basal part. Base of wing slightly shaded with yellow. Wing narrow and long. Hind wing (fig. 4) half as wide as long. Costal space reaches nearly to apex of wing, and cross veins are present only in apical half. Rs arises about half-way along the wing, and MP is forked just basally to this. *Legs:* Femur light brown with two dark brown bands, tibia with one dark band. Fore legs are missing in holotype and paratypes. Tarsal segments of middle and hind legs in descending order of length are 5, 2, 3 = 4, 1 (fused with tibia). Tarsal claws all sharp. *Genitalia* (fig. 33): Light brown. Penis large and protrudes beyond the narrowing of first segment of forceps. Appendix dorsalis well developed.

Female imago.—Resembles male. Subanal plate bears a deep semicircular incision.

Subimago.—Wings grey with well-marked brown cross veins, which give a slightly mottled appearance. Imaginal colouring of C. and Sc areas shows beneath the grey colour.

Nymph.—Measurements : Body-length 11 mm. (10–12 mm.). *General colour :* Yellowish brown to dark brown. *Mouthparts* (fig. 27–31) : Labrum bears five denticular plates which are larger than those of other known Australian *Atalophlebia*. Mandibular teeth more pointed than those of other specimens of this genus. *Gills* (fig. 26) : Feathery in appearance, forming a thick mat on either side of abdomen, making nymph appear much broader than it really is. *Legs :* Two transverse dark bands present on femur and tibia. Tarsus generally darker than rest of leg.

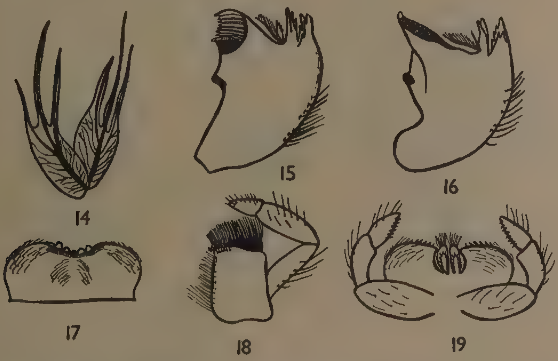
Specimens examined, nymphs and imagines, NEW SOUTH WALES : Newcastle, Kahibah, 100 ft., xii.1948, from rock pools (*B. McMillan*). N.S.W.: Barrington Brush, 1350 ft., 8.viii.1948, from stagnant pools (*B. McMillan*). N.S.W. : Cooronbong, 50 ft., 9.xii.1948 (*B. McMillan*). N.S.W. : Narrabeen, ix.1948 (*B. McMillan*).

Imagines. N.S.W. : Hampton, i.1948 (*R. J. Tillyard*). N.S.W. : Bolaro, 10.xi.1936 (*R. J. Tillyard*). SOUTH AUSTRALIA : Mt. Gambier, 9.xi.1934 (*R. J. Tillyard*). N.S.W. : Epping (*R. J. Tillyard*) and x.1948 (*J. Harker*).

Atalophlebia maculosa Harker.

The nymphs and subimagines of this species were previously unknown.

Nymph.—Measurements : Body length 8·0 mm. (7·0–8·5 mm.) *General colour :* Black with some yellow. *Mouthparts :* See figs. 15–19. *Legs :* Two black bands on both femur and tibia, most of tarsus black. Tarsal claws yellow. *Gills* (fig. 14) : Trifurcate. Cerci banded with black.



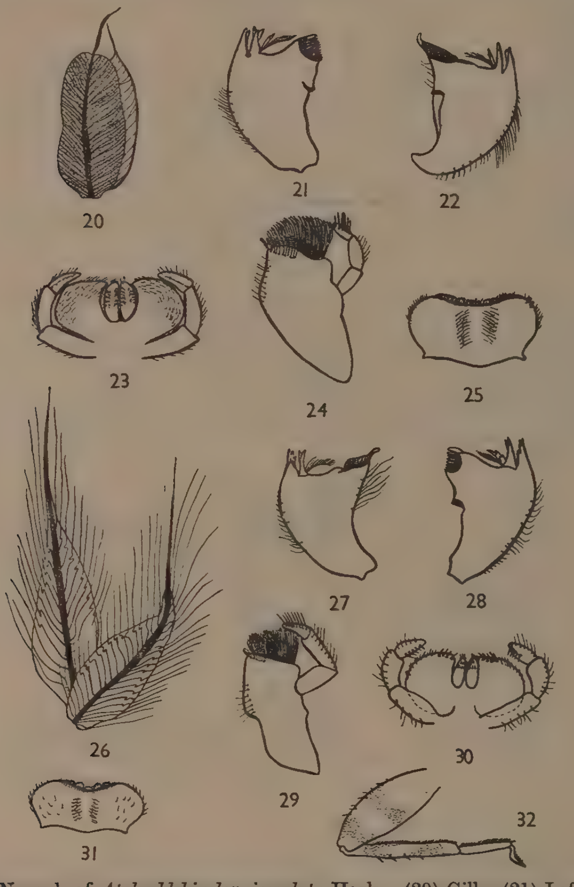
FIGS. 14–19.—Nymph of *Atalophlebia maculosa* Hark. (14) Gill. (15) Left mandible. (16) Right mandible. (17) Labrum. (18) Maxilla. (19) Labium.

Subimago.—Measurements : Body-length 9 mm. (8·5–10 mm.). *Wings :* Dark brown. All cross veins heavily shaded so that wing appears dark brown, but the very small lighter areas between the cross veins give a speckled appearance on closer examination. Imaginal colouring appears beneath subimaginal cuticle.

Atalophlebia longicaudata Harker.

The nymph of this species was previously unknown.

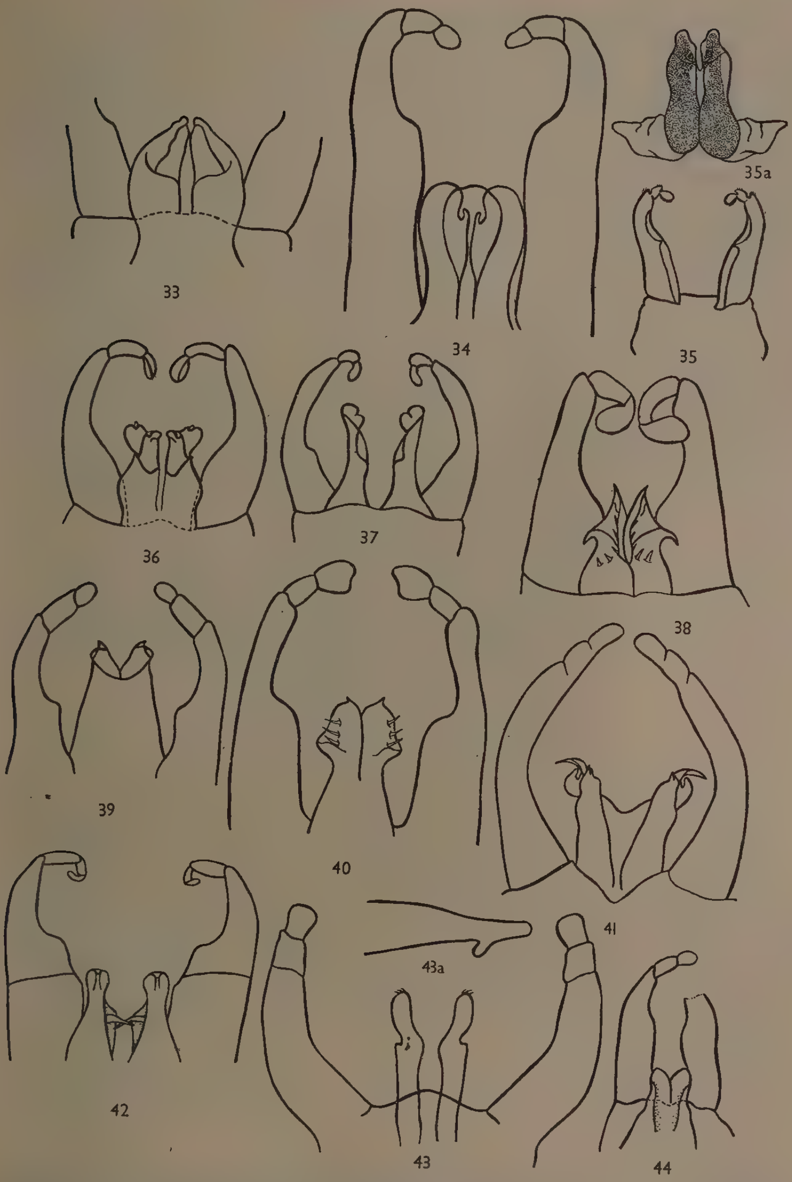
Nymph.—Measurements : Body-length 10 mm. (9·5–11 mm.). *General colour :* Dark brown to black. *Mouthparts :* See figs. 21–25. *Legs :* Femur very broad, being about five times as broad as tibia and tarsus. Legs yellowish in colour with a broad black mark at distal end of femur, proximal end of tibia and central region of tarsus. In some specimens all these black markings are doubled. Tarsal claw with a black tip. *Gills* (fig. 20): Outer lamella broad, black with a long hair-like tip, inner lamella pale and transparent, and adheres closely to outer lamella.



Figs. 20–32.—Nymph of *Atalophlebia longicaudata* Hark. (20) Gill. (21) Left mandible. (22) Right mandible. (23) Labium. (24) Maxilla. (25) Labrum. Nymph of *Atalophlebia australasica* (Pict.). (26) Gill. (27) Right mandible. (28) Left mandible. (29) Maxilla. (30) Labium. (31) Labrum. (32) Leg.

Specimens examined, New South Wales: Barrington, Tops R., 4700 ft., 27.iii.1948 (*B. McMillan*). N.S.W.: Armidale, Commissioners Waters, 3000 ft., 1.xii.1948.

The species of *Atalophlebia* found in Eastern Australia form a closely related group. When the nymphs are considered, however, one species, *A. longicaudata*, may appear to have less affinity with the genus than the others, due to the



FIGS. 33–44.—Male genitalia. (33) *Atalophlebia australasica* (Pict.). (34) *Atalophlebia tuhla* sp. n. (35) Forceps of *Atalophlebia miunga* sp. n. (35*a*) Penis of *Atalophlebia miunga* sp. n. (36) *Atalophlebia kala* sp. n. (37) *Atalophlebia pierda* sp. n. (38) *Deleatidium decipiens* sp. n. (39) *Deleatidium bundutum* sp. n. (40) *Deleatidium pusillum* sp. n. (41) *Atalomicria uncinata* (Ulm). (42) *Kirrara amenia* sp. n. (43) *Kirrara procera* sp. n. (43*a*) *Kirrara procera.* Lateral view of penis. (44) *Deleatidium nanatum* sp. n.

presence of a gill which is not furcated. Repeated observation has shown that the multifurcate gills of the rest of the genus have no fixed number of furca; those with large numbers vary greatly, those with three are more stable but are at times observed to have more than three. Since the furca themselves are merely divisions of a gill enclosing a tracheal branch, and the flat part of the lamella contains similar branches but does not divide around them, it is possible that more furca can be formed by the splitting back of the gill tissue. The plate-like gill of *A. longicaudata* is similar in appearance to the lamella of the multifurcate gills and can be seen to have similar branching trachea. Already the central trachea has been produced beyond the gill plate. It would seem that a series of gills appears in this genus with either the gradual production of many furca from the flat gill of *A. longicaudata*, through the trifurcate gill of *A. maculosa* to the much divided gill of *A. australasica*, or that the gills are gradually losing their division and becoming more plate-like. The former series is the more likely when compared with the general trends within the Ephemeroptera and also increases the respiratory surface, as the increasing division of the gill prevents to some extent the settling of silt on the surface, an important factor in streams which become very low in summer.

There is a close correlation between the increased division of the gills and the habitat, as can be seen from the following table:

Nymph.	*Gill.*	*Habitat.*
A. longicaudata	Broad, single plate	Wide streams, medium or fast flow.
A. maculosa	Trifurcate	Swifter parts of streams.
A. incerta	,,	Swifter parts of streams.
A. australis	Multifurcate	Under rocks or debris.
A. costalis	,,	Under rocks
A. australasica	Feathery, much divided	Stagnant pools.

Atalomicria gen. n.

Male imago.—Wings: Fore wing long and narrow like that of *Atalonella*, but cross veins are present and well developed in basal half of costal area. CuP of fore wing strongly curved. Hind wing has a distinct costal hump, but costal space is long and narrow. MP forked, and an intercalary present. MA arises at about half to two-thirds of distance from base to apex, and Rs arises at, or near, the same place. *Legs:* Tarsal claws of each pair similar and sharp. Tarsi appear to be four-segmented owing to fusion of first segment with tibia. *Genitalia:* Penis of male has an appendage near each orifice. Forceps three segmented with a long basal segment and two short distal segments. Basal segment narrows gradually, if at all, and not abruptly as in *Atalophlebia*.

Nymph.—Unknown.

Type species.—Atalomicria uncinata (Ulmer)

To this genus the following species is now referred.

Atalomicria sexfasciata (Ulmer) **comb. nov.**

This genus is close to both *Atalonella* and *Atalophlebia*, bearing a few characters of each, but the genitalia are quite distinctive.

It should be noted that in Ulmer's, 1917, figure of the hind wing of *A. uncinata* and *A. sexfasciata* there is no intercalary shown in the fork of MP. Of the forty-three specimens examined by the author all had an intercalary in this fork.

A new text-figure (fig. 41) of the genitalia of *A. uncinata* is given. The penis of this species is curved slightly in the dorso-ventral plane, so that when the genitalia are mounted on a slide the cover slip presses the two halves of the penis on their sides. Ulmer's figure (1917) shows one angle only, and therefore this new figure is included, showing the further elaboration of the penis on the other side.

Ulmer's figure of the fore wing shows shading only in the pterostigmatal area, but in some of the specimens examined the whole of the costal and subcostal areas is yellow, and the pterostigmatal area is reddish.

Genus *Deleatidium* Eaton, 1899.

The nymphs of only three species have been determined, and all three have double gills. Phillips (1930), finding the same problem in New Zealand nymphs, placed species with double gills in the subgenus *Atalophlebiodes*. Ulmer (1938) and Traver (1946) both consider the subgenus to be worthy of generic rank; they distinguish certain features of venation which separate the imagines of two Brazilian species, *A. haruupi* and *A. sao-paulense*, from *Deleatidium*. These venational characters do not appear to be present in the Australian members of *Atalophlebiodes*, and marked differences are apparent in the hind wing of the Australian and Brazilian representatives. It is possible that the Brazilian species do not belong to this group at all. Since the imagines of the Australian *Atalophlebiodes* cannot be distinguished from those of *Deleatidium*, it is proposed that the latter should still be regarded as a subgenus.

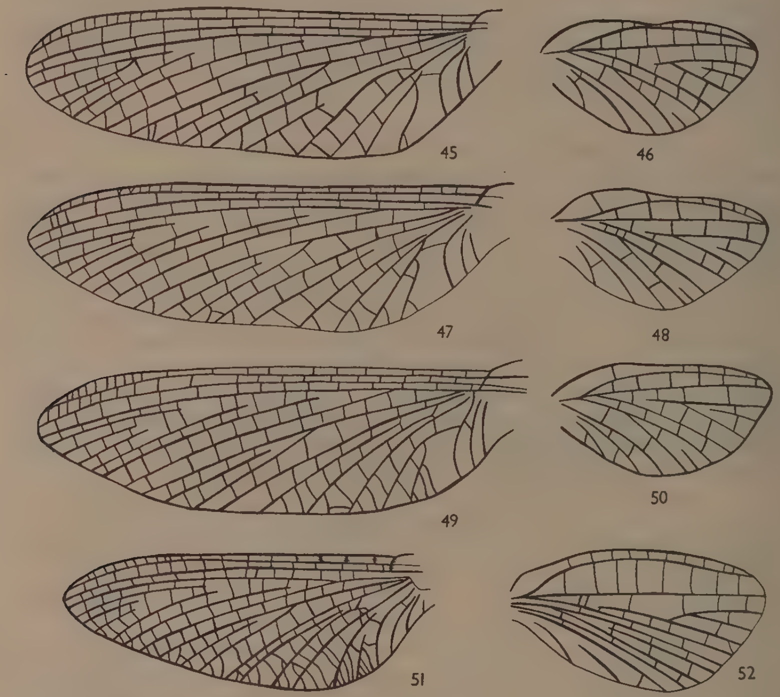
KEY TO IMAGINES.

1. Penis not reaching as far as narrowing of first segment of forceps . . 2.
   Penis reaching up to, or beyond, narrowing of first segment of forceps 4.
2. Penis boot-shaped . . . . **D. mjobergi** (Ulm.)
   Not so . . . . 3.
3. Penis deeply divided. Forceps base with a central convex projection **D. strigata** (Eat.)
   Penis only slightly divided. Forceps base slightly concave in the central region . . . . **D. nanatum** sp. n.
4. Penis only slightly divided . . . . 5.
   Penis divided almost to base . . . . 6.
5. Distal end of penis with two outwardly curved tips . **D. bundutum** sp. n.
   Not so . . . . **D. crassa** (Harker)
6. Penis rounded at tip . . . . **D. unguicularis** (Ulm.)
   Penis not rounded at tip . . . . 7.
7. Penis flattened at tip . . . . **D. annulatum** (Harker)
   Penis acute at tip . . . . 8.
8. Lateral edges of penis curved to form a hook-like projection **D. decipiens** sp. n.
   Lateral edges of penis rounded . . . . **D. pusillum** sp. n.

Deleatidium pusillum sp. n.

Male imago.—Measurements: Fore wing 8 mm. Hind wing 2 mm. *General colour:* Yellow brown with light brown markings. *Wings:* Veins yellow. In the fore wing (fig.

51) cross veins in basal region of costal and subcostal area darker than elsewhere. In the hind wing (fig. 52) costal area relatively wide with a number of cross veins. Rs arises close to wing base and fork of MP is basal even to this. *Legs :* Brown without any distinct marking. In the fore leg tibia and tarsus about equal in length, being slightly longer than femur. Tarsal segments in descending order of length are 2, 3, 4, 5, 1 (fused with tibia). In middle and hind legs order of tarsal segments is 5, 4, 3, 2 = 1 (fused with tibia). Of each pair of tarsal claws one is blunt and the other acute. *Genitalia* (fig. 40) : Forceps light brown except for second segment, which is dark brown. Penis long, reaching beyond the narrowing of first segment of forceps. Cerci light brown with narrow dark bands on each segment.



Figs. 45–52.—Imaginal wings. *Deleatidium nanatum* sp. n. (45) Fore wing. (46) Hind wing. *Deleatidium decipiens* sp. n. (47) Fore wing. (48) Hind wing. *Deleatidium bundutum* sp. n. (49) Fore wing. (50) Hind wing. *Deleatidium pusillum* sp. n. (51) Fore wing. (52) Hind wing.

Female imago.—Subanal plate V-shaped without an incision.

Subimago.—Wings grey to brown without any shading ; cross veins dark brown.

Holotype male, allotype female, morphotype subimago, New South Wales : Bolaro, 10.ii.1936 (*R. J. Tillyard*). All types in British Museum (Natural History), pinned and set.

Deleatidium decipiens sp. n.

Male imago.—Measurements : Fore wing 10 mm. Hind wing 3 mm. *General colour :* Light brown with dark brown markings. *Wings :* Veins yellow. In the fore wing (fig. 47) pterostigma slightly opaque. Cross veins in costal area, and in basal portion of wing, slightly darker than elsewhere. In the hind wing (fig. 48) costal area long with a deep concavity at about half its length from base to apex. Rs arises close to wing base, and fork of MP very close to wing base. *Legs :* Brown without any distinctive markings. In the fore legs tarsal segments in descending order of length are 2 = 3, 4, 5, 1 (fused with tibia). In the middle and hind legs order of tarsal segments is 5, 2 = 3, 4, 5, 1 (fused with tibia). Of each pair of tarsal claws one is sharp and the other blunt. *Genitalia* (fig. 38) : Forceps yellow except for second segment, which is brown. Penis large, reaching past the narrowing of first segment of forceps. Cerci light brown ; appendix dorsalis well developed.

Female imago.—Subanal plate large and oval with no incision.

Subimago.—Wings of a uniform grey colour without shading, but the well-marked cross veins give a slightly mottled appearance.

Holotype male, morphotype subimago, NEW SOUTH WALES : Upper Murrumbidgee, Adaminaby, 11.xii.1936 (*R. J. Tillyard*). Allotype female and paratypes, N.S.W. : Mount Kosciusko, Spencers Creek, 6000 ft., 2.i.1933 (*R. J. Tillyard*).

All types in British Museum (Natural History), pinned and set.

Deleatidium nanatum sp. n.

Male imago.—Measurements : Fore wing 8 mm. Hind wing 2 mm. *General colour :* Yellowish with brown markings. *Wings :* Veins yellow. In the fore wing (fig. 45) cross veins towards base of wing darker than those in any other part except the pterostigmatal area. Brace vein dark brown where it crosses Sc. Hind wing (fig. 46) has a long narrow costal region with few cross veins. Fork of MP arises close to base of wing, origin of Rs being apical to this fork. *Legs :* Brown without any distinctive markings. Tibia of fore legs distinctly longer than femur and tarsus. Tarsal segments in descending order of length in the fore leg are 2 = 3, 4, 5, 1. In the middle and hind legs order of tarsal segments is 5, 4 = 3 = 2, 1 (fused with tibia). One tarsal claw of each pair sharp, the other blunt. *Genitalia* (fig. 44) : Forceps yellowish and large. Penis dark in colour and short, not reaching more than half-way up the broad part of first segment of forceps. Appendix dorsalis well developed and each of its segments, and those of the cerci, distinctively banded with dark brown.

Subimago.—Wings brown, with each cross vein shaded with darker brown, giving wing a slightly banded appearance.

Female, imago, nymph.—Unknown.

Holotype male, morphotype subimago, NEW SOUTH WALES : Upper Murrumbidgee, Adaminaby, 11.xii.1926 (*R. J. Tillyard*).

Deleatidium (*Atalophlebiodes*) *annulatum* Harker.

To the forms previously described the description of the nymph can now be added :

Nymph.—Measurements : Body-length 12 mm. (11–13·5 mm.). *General colour :* Dark brown. *Mouthparts :* Maxilla with three-segmented palp, distal segment of which is about the same size as middle segment ; in this respect the nymph differs from the New Zealand species with their very small distal segments. Mandible with a broad molar region and very narrow incisors. *Gills :* Lanceolate, double.

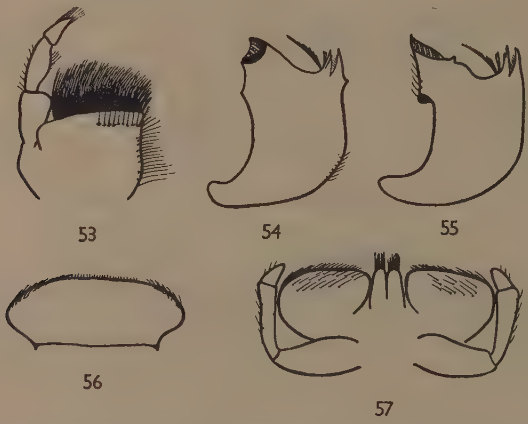
Specimens examined, New South Wales : Barrington R., 4600 ft., 27.iii. 1948 (*B. McMillan*). N.S.W. : Glen Innes, Beardy River, 3520 ft., iii.1948.

Deleatidium (*Atalophlebiodes*) *crassa* (Harker) **comb. nov.**

Re-examination of this species shows that it belongs to *Deleatidium* and not *Leptophlebia*, the genus in which it was originally placed.

Deleatidium (Atalophlebiodes) bundutum sp. n.

Male imago.—Measurements : Fore wing 10 mm. Hind wing 3 mm. *General colour :* Yellow with brown markings. *Wings* (figs. 49, 50) : Veins light brown without any shading of cross veins. Costal area of hind wing long and narrow. Rs arises about about half-way between wing base and apex, and fork of MP slightly basal to this. *Legs :* Yellowish with two dark brown bands on femur. In fore legs tarsus slightly longer than tibia, which is longer than femur ; tarsal segments in descending order of length are 2 = 3 = 4, 5, 1 (fused with tibia). Order of the tarsal segments in mid and hind legs is 5, 2, 3 = 4, 1 (fused with tibia). Of each pair of tarsal claws one is sharp and the other obtuse. *Genitalia* (fig. 39) : Penis only partly bisected, and reaches beyond the narrowing of first segment of forceps. Cerci light brown.



Figs. 53–57.—Nymphal mouthparts of *Deleatidium bundutum* sp. n. (53) Maxilla. (54) Left mandible. (55) Right mandible. (56) Labrum. (57) Labium.

Subimago.—Wings yellow-brown, very similar to imago.

Nymph.—Measurements : Body-length 14 mm. *General colour :* Yellow with dark brown markings. *Mouthparts* (figs. 53–57) : Free edge of labrum straight and not denticulate. Mandibular teeth very small and narrow relative to size of whole mandible. *Gills :* Lanceolate and double. *Legs :* Yellowish with darker regions on ventral half of femur. A very distinctive cream patch at apical end of femur.

Holotype male, morphotype subimago, New South Wales : Armidale, Dumaresque Cr., 3000 ft., 6.vii.1948. Morphotype nymph, N.S.W. : Barrington, Williams R., 1150 ft. 8.viii.1948 (*B. McMillan*).

The nymphs of *Deleatidium* (*Atalophlebiodes*) all live in the swifter parts of streams, and it is interesting to note in this connection the lanceolate gill and rounded form of body. Attention has been drawn (p. 252) to the correlation between gill shape in *Atalophlebia* and the rate of water flow. Nymphs of *Deleatidium* exhibit the undivided gill in its simplest form.

Jappa gen. n.

Male imago.—Wings : Fore wing has numerous cross veins, particularly in subcostal space, where they are upright and parallel. like those in the closely related genus *Deleatidium.* MP_2 strongly bowed to rearward at its junction with MP_1. Proportions of fore wing markedly different from those of *Deleatidium,* the wing being about five times as long as wide, as compared to twice to three times as long as wide in *Deleatidium.* Hind wing has a long narrow costal region with numerous cross veins, MP forked, and intercalary may be absent or very small. *Thorax :* Pronotum much longer than that of any other Australian member of the Leptophlebiidae. *Genitalia :* Penis much longer than that of *Deleatidium* and deeply bilobed, the two halves appearing to be completely separated in most specimens. Forceps are three segmented, with the basal segment very long, and the other two very short.

Nymph.—A burrowing type. Head large with lateral eyes, and with two tusk-like projections on either side of labrum. Labrum has a convex projection in middle of free border, not a concavity as in related genera. Maxillary palp two-segmented, with distal segment large and almost rectangular in outline.

Type species :—*Jappa kutera* sp. n.

Jappa kutera sp. n.

Male imago.—Measurements : Fore wing 12 mm. (11·5–12·5 mm.). Hind wing 2·5 mm. *General colour :* Red brown with dark red or black markings. *Wings :* Veins dark brown to red brown. In the fore wing (fig. 64) cross veins in costal and subcostal areas shaded with brown, and whole of this area is an opaque golden brown. MP_2 is noticeably bowed, slanting towards CuA, to which it is joined by a cross vein. In the hind wing (fig. 65) costal area is long and narrow with cross veins along its length. Rs arises at about half length of wing, and fork of MP is slightly basal to this. A small intercalary present in fork of MP. *Legs :* Cream, or golden brown, without any markings. Tarsus of fore legs slightly longer than tibia, which is longer than femur. Tarsal segments in descending order of length are 3, 2 = 4, 5, 1 (fused with tibia). In the middle and hind legs order of tarsal segments is 5, 2 = 3 = 4, 1 (fused with tibia). Of each pair of tarsal claws one is blunt and the other sharp. *Genitalia* (figs. 67–68) : Forceps and penis light brown. Penis very long, but not reaching beyond the narrowing of first segment of forceps. First segment of forceps narrows suddenly giving a right-angle edge. Cerci ringed with red brown. Appendix dorsalis well developed.

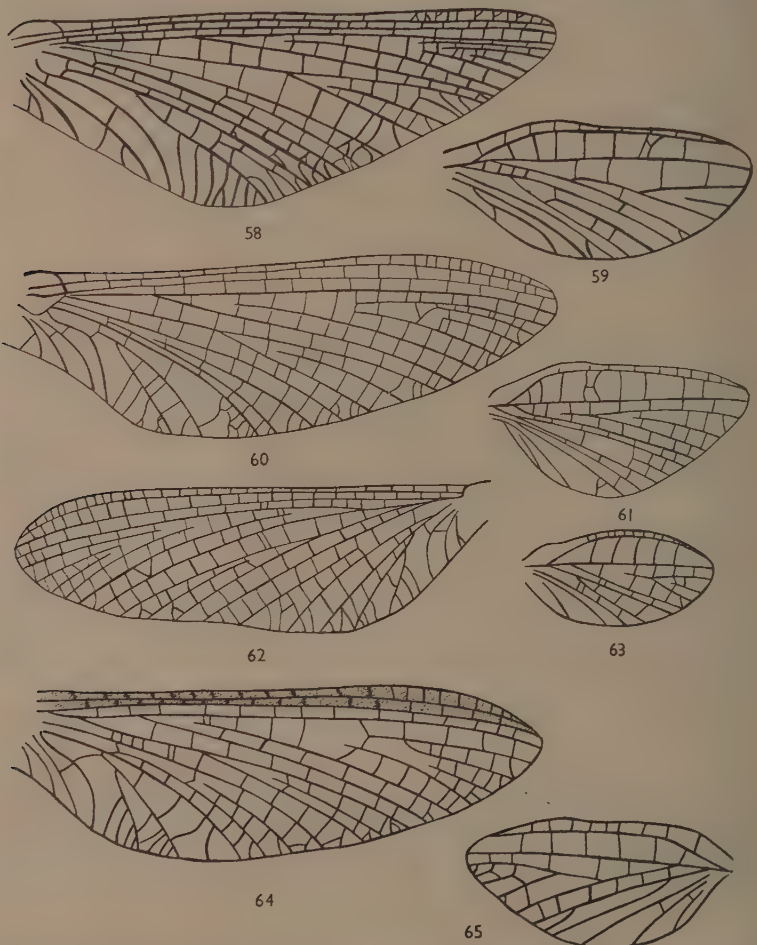
Female, imago and nymph.—These have been described in the appendix to a previous paper (Harker, 1950, p. 31).

Holotype male, NEW SOUTH WALES : Armidale, 3000 ft., xi.1948. Allotype female, morphotype subimago and nymph, N.S.W. : Armidale, i.1948. In the Australian Museum Collection, in spirit. Other specimens examined, QUEENSLAND : Eidswold, 27.ix.1929, 20.ix.1929, 10.ix.1929 (*R. J. Tillyard*). In British Museum Collection, N.S.W. : Tarana, Fish R. (*B. McMillan*). N.S.W. : Tumut, 24.xii.1947 (*B. McMillan*).

Jappa tristis sp. n.

Male imago.—Measurements : Fore wing 10 mm. Hind wing 3 mm. *General colour :* Golden brown with dark brown markings. *Wings :* Veins golden brown. In the fore wing (fig. 62) cross veins in basal part of costal and subcostal areas very faint, those in pterostigmatic area noticeably upright as compared with the more usual slanting veins in this region. In the hind wing (fig. 63) costal area relatively wide and long with a number of cross veins. Rs arises in apical third of wing, and fork of MP quite close to base of wing. *Legs :* Golden brown without markings. Fore legs are missing in all specimens. Tarsal segments in middle and hind legs in descending order of length are 5, 2 = 3, 4, 1 (fused with tibia). Of each pair of tarsal claws one is blunt and the other acute. *Genitalia* (fig. 66) : Forceps and penis light brown. Penis long, reaching almost to the end of first segment of forceps. Cerci light brown. Appendix dorsalis well developed.

Female Imago.—Subanal plate large with an almost straight tip.



FIGS. 58–65.—Imaginal wings. *Kirrara procera* sp. n. (58) Fore wing. (59) Hind wing. *Kirrara amenia* sp. n. (60) Fore wing. (61) Hind wing. *Jappa tristis* sp. n. (62) Fore wing. (63) Hind wing. *Jappa kutera* sp. n. (64) Fore wing. (65) Hind wing.

Holotype male, allotype female, TASMANIA: Cradle Mt., 21.i.1917 (*R. J. Tillyard*). In the British Museum (Natural History), pinned and set.

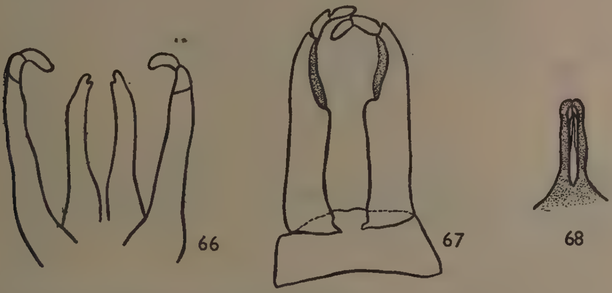
Kirrara gen. n.

Imago.—Wings: Intercalaries in posterior half of fore wing all arise further in towards base than in any other Australian genera. In particular the first intercalary of CuA arises midway between CuA_1 and CuP_1, giving the appearance of another main vein. From the second intercalary of CuA a pectinate series of veins descends to the tornus, resembling the veins in members of the Siphlonuridae, but, unlike that family, CuA does not end at the tornus. Costal area of hind wing narrow and elongate, with a shallow depression at half its length. No fork on MA, and a triad is formed on MP. *Legs:* Tarsi four-segmented, and tarsal claws of each pair are unlike. *Genitalia:* Forceps three-segmented with the narrowing of first segment occurring close to base. Appendix dorsalis well developed.

Type species:—*Kirrara procera* sp. n.

Kirrara procera sp. n.

Male imago.—Measurements: Fore wing 18 mm. Hind wing 4 mm. *General colour:* Golden brown. In the fore wing (fig. 58) C and Sc spaces dark golden brown. First intercalary of CuA arises further in towards wing base than that of any other Australian Leptophlebiid, and a number of descending veins run from the second intercalary to the tornus, rather after the manner of those in the Siphlonurids. Costal space of hind wing (fig. 59) long and narrow with a number of cross veins. Rs arises close in towards wing base, and fork of MP slightly basal to this. *Legs:* Yellow brown with darker markings except for a slightly darker region at each joint. In the fore legs, tibia and femur about equal in length. In the hind legs tibia slightly longer than femur. Tarsal segments in descending order of length are 5, 2, 3 = 4, 1 (fused with tibia). Tarsal claws of each pair unlike, one being sharp and the other blunt. *Genitalia* (fig. 43): Forceps three-segmented, first segment narrowing gradually from base to apex. The two halves of penis well separated, and reaching as far as beginning of second segment of forceps. Appendix dorsalis well developed.



FIGS. 66–68.—Male genitalia. (66) *Jappa tristis* sp. n. *Jappa kutera* sp. n. (67) Forceps. (68) Penis.

Female imago.—Subanal plate V-shaped with a very small incision at the free end.

Subimago.—Wings grey with imaginal colouring showing through the subimaginal skin.

Holotype male, allotype female, NEW SOUTH WALES: Upper Murrumbidgee R., Adaminaby, 2.xii.1936 (*R. J. Tillyard*). Morphotype subimago, N.S.W.: Bolaro, 10.ii.1936 (*R. J. Tillyard*). Other specimens examined. N.S.W.: Tumut-Talbingo Road, 24.xii.1947, in heavy rain (*B. McMillan*).

Kirrara amenia sp. n.

Male imago.—Measurements: Fore wing 13 mm. (12–14·5 mm.). Hind wing 3 mm. *General colour:* Brown with yellowish brown markings. *Wings:* Veins light yellowish brown with Sc, R_1, and MA slightly darker in fore wing, and Sc darker in hind wing. Base of fore wing faintly clouded with yellow, costal and subcostal spaces being slightly opaque, and cross veins in this region being darker than elsewhere. Fore wing (fig. 60) has a relatively long region basal to tornus, giving a triangular appearance to the wing. Hind wing (fig. 61) about two-thirds as wide as long. Costal area long and relatively wide compared with the previous species, and has a number of cross veins along its length. Rs arises close to wing base; MP forked very close to wing base. *Legs:* Brown without any distinctive marking, femur being slightly darker than tibia and tarsus. In the fore leg femur and tibia about equal in length and tarsus slightly longer; tarsal segments in descending order of length 2 = 3, 4, 5, 1 (fused with tibia). In the middle and hind legs order of tarsal segments is 5, 2 = 3, 4, 1 (fused with tibia). Tarsal claws all sharp. *Genitalia* (fig. 42): Brown with three segmented forceps, of which the last two segments are slightly lighter. Penis small and deeply bisected, reaching only to end of the wide region of first segment of forceps. Cerci brown with a slightly darker ring at end of each segment; appendix dorsalis well developed.

Female imago.—Generally resembling male, but with a slightly shorter, heavier body. Subanal plate large and oval with no incision.

Subimago.—General coloration dull brown. Wings a uniform grey without any shading.

Nymph.—Unknown.

Holotype male, allotype female, morphotype subimago and paratypes, NEW SOUTH WALES: Mt. Kosciusko, Spencers Cr., 6000 ft., 20.xii.1932 (*R. J. Tillyard*). In the British Museum (Natural History), all types pinned and set.

Notes on the Leptophlebiidae.

Leptophlebiidae is the dominant family of the Australian mayfly fauna. It appears to have invaded similar habitats to those occupied in Europe by other families. Together with this invasion of habitats unusual for the Leptophlebiids, the nymphs show morphological adaptations similar to those elsewhere recognised as peculiar to other families. The most striking example of this convergence of morphological adaptation appears in the new genus *Jappa*, which is closely similar in the nymphal stage to the genus *Ephemera*. Both nymphs are burrowing forms with curved tusk-like projections on the head, being formed on either side of the labrum in *Jappa*, and on the mandibles in *Ephemera*; the gills are feathery and lie above the abdomen in both genera, and the fore legs are modified for digging.

Another example of this convergence appears in an, as yet, undescribed genus, of which the nymph only has been found. This nymph (figs. 80–90) is so closely similar to nymphs of *Rithrogena* that it was at first thought to belong to this genus, but closer examination shows that the mouthparts are of the Leptophlebiid type, as are the veins showing through the wing pads. The gills in this nymph are, like those of *Rithrogena*, modified to form a sucker underneath the abdomen, and their individual form is closely related to that of the latter genus.

3. SIPHLONURIDAE.

Mirawara gen. n.

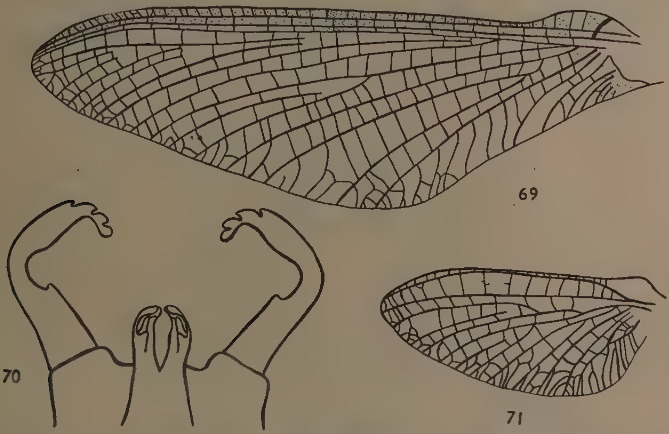
Imago.—Wings : Fore wing like that of genus *Coloburiscoides* Lestage, with MP$_2$ normally attached to MP$_1$. Costal margin of hind wing slightly angulated near the base. MA and MP distinctly forked. *Legs :* Tarsi of all legs distinctly five-segmented. One of each pair of tarsal claws blunt, the other acute. *Genitalia :* Forceps four-segmented, with basal joint long and narrowing abruptly at about half its length. *Abdomen :* Last abdominal segment backwardly projected at its posterior lateral edge. Appendix dorsalis completely aborted.

Type species :—*Mirawara aapta* sp. n.

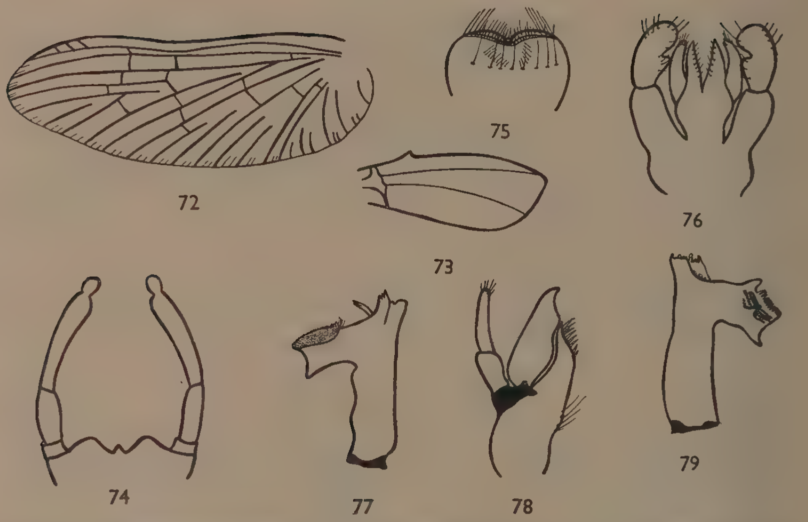
This genus is probably close to *Coloburiscoides*, but the four segmented forceps distinguish it clearly from this group.

Mirawara aapta sp. n.

Male imago.—Measurements : Fore wing 19 mm. Hind wing 9 mm. *General colour :* Golden brown with dark brown markings. *Wings :* Veins dark brown. In the fore wing (fig. 69) C and Sc areas golden brown with two slightly darkened regions, one directly above the fork of Rs, and the other on a level with the forking of MA. MP$_2$ is normally attached to MP$_1$. Costa of hind wing has a slight angulation near the base. MP forks on a level with the origin of Rs. *Legs :* Femur of fore legs longer than tibia, and together they are about equal to tarsi. Tarsal segments in descending order of length are 1 = 2 = 3, 4, 5. Femur of hind leg slightly shorter than tibia, and about equal to tarsi. Tarsal segments in descending order of length are 1 = 2, 3, 4, 5. Of each pair of tarsal claws one is acute and the other blunt. *Genitalia* (fig. 71): Forceps four-segmented; basal joint narrows abruptly at about half its length, and apical three small joints are divided by well-marked V-shaped concavities. Penis does not reach beyond the narrowing of first segment of forceps. *Abdomen :* Tenth abdominal segment bears a long backwardly directed projecting spine. Appendix dorsalis is aborted.



FIGS. 69–71.—*Mirawara aapta* sp. n. (69) Imaginal fore wing. (70) Imaginal hind wing. (71) Male genitalia.



Figs. 72–79.—*Baetis sogeriensis* sp. n. (72) Imaginal fore wing. (73) Imaginal hind wing. (74) Male genitalia. (75) Labrum. (76) Labium. (77) Right mandible. (78) Maxilla. (79) Left mandible.

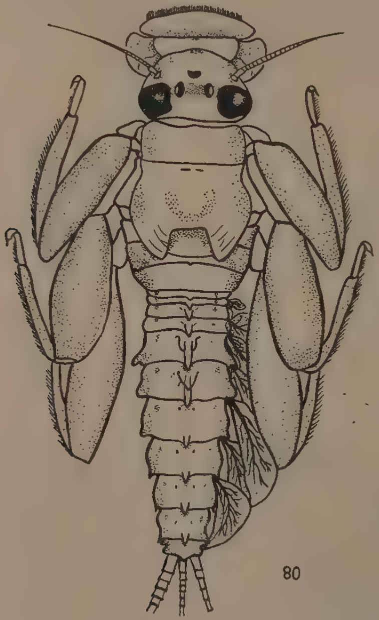


Fig. 80.—Nymph of Leptophlebiid, genus (?).

Female imago.—Posterior lateral edges of all abdominal segments slightly elongated, and abdomen more flattened than that of male. Subanal plate W-shaped.

Subimago.—Wings grey with all cellules slightly shaded. A lighter band apparent halfway between tornus and apex, running between costa and MP_2.

Holotype male, allotype female, morphotype subimago, N.S.W.: Upper Murrumbidgee, Adaminaby, 11.xii.1936 (*R. J. Tillyard*).

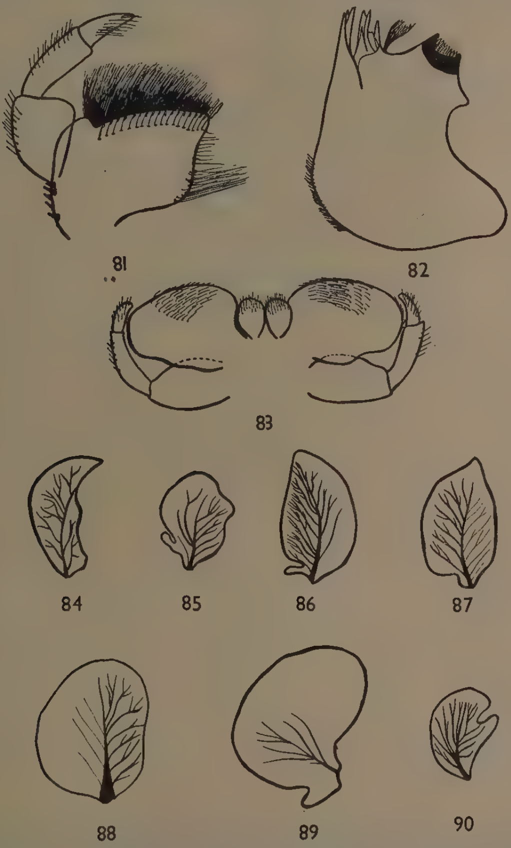
4. Baetidae.

Baetis Leach.

Baetis confluens Harker.

To the previous description that of the nymph of this species can now be added:—

Nymph.—Measurements: Body-length 10 mm. (8–11 mm.). *General colour:* Light brown. *Mouthparts:* Labrum deeply notched in middle region of free margin, and bears



Figs. 81–90.—Nymph of Leptophlebiid, genus (?). (81) Maxilla. (82) Left mandible. (83) Labium. (84–90) Gills 7–1.

more hairs than that of *B. baddamsae* Harker. Left mandible bears a strong blunt projection just below molar edge, which is absent in *B. baddamsae*. Labial palp notched on inner edge of distal segment, but not as deeply as that in *B. baddamsae*. *Legs :* Light yellowish brown with a dark patch on dorsal region of femur. Distal ends of tibia and tarsus marked with a dark line.

Morphotype, NEW SOUTH WALES : Barrington, Williams R., 1500 ft., 29.iii.1944 (*B. McMillan*). Paratype, N.S.W. : Armidale, Commissioners Waters, 3000 ft. 20.i.1945.

Baetis sogeriensis sp. n.

Male imago.—Measurements : Fore wing 4 mm. Hind wing 0·5 mm. *General colour :* Creamy yellow with a darker head and tip of abdomen. *Wings :* Wings clear. In the pterostigmatic area of the fore wing (fig. 72) are a few scattered cross veins, no others occur in costal area. Hind wing (fig. 73) reduced, with only two very weak veins ; a costal spur present. *Abdomen :* Segments one to six very pale and transparent with a brown band at posterior end of each. Segments seven to ten brown and opaque. *Genitalia :* (fig. 74) Basal segment of forceps slightly shorter than second, and with a very slight swelling on inner side. Third segment very small, globular and incompletely divided from second.

Holotype male and paratypes, NEW GUINEA : Sogeri, near Port Moresby, 1.vi.1947 (*R. Wharton*). Imagines and subimagines found on the walls of a latrine.

5. CHECK-LIST OF AUSTRALIAN SPECIES.

LEPTOPHLEBIIDAE.

Atalomicria gen. n. Type-species *A. uncinata* (Ulmer).
- *sexfasciata* (Ulmer), 1917, in *Atalophlebia*. **Comb. nov.** Type : Stockholm Museum.
- *uncinata* (Ulmer), 1917, in *Atalophlebia*. **Comb. nov.** Type : Stockholm Museum.

Atalonella Needham and Murphy, 1924. Type-species *A. ophis* (?). Needham and Murphy.
- *brunnea* (Tillyard), 1935, in *Atalophlebia*. **Comb. nov.** Type : British Museum.
- *delicatula* (Tillyard), 1935, in *Atalophlebia*. **Comb. nov.** Type : British Museum.
- *fuscula* (Tillyard), 1935, in *Atalophlebia*. **Comb. nov.** Type : British Museum.
- *lucida* (Ulmer), 1919, in *Atalophlebia*. **Comb. nov.** Type : Stockholm Museum.
- *parva* (Harker), 1950, in *Atalophlebia*. **Comb. nov.** Type : Australian Museum.
- *simillima* (Ulmer), 1919, in *Atalophlebia*. **Comb. nov.** Type : Stockholm Museum.

Atalophlebia Eaton, 1881. Type-species *A. australis* (Walker). Redescribed by Tillyard, 1933.
- *albiterminata* Tillyard, 1935. Replaces *A. costalis*. Type : Unknown.
- *australasica* (Pictet), 1843, in *Baetis*. To *Leptophlebia* Eaton, 1871, *Atalophlebia* Eaton, 1888. Type : Unknown.

australis (Walker), 1853, in *Ephemera.* To *Leptophlebia* Eaton, 1871, *Atalophlebia* Eaton, 1881. Redescribed Tillyard, 1933. Type: British Museum.

**brunnea* (Tillyard), 1935. To *Atalonella.* Type: British Museum.

**costalis* (Burmeister), 1839, in *Baetis.* To *Potomanthus* Pictet, 1853, *Leptophlebia* Eaton, 1871, *Atalophlebia* Eaton, 1888. Hononym *B. costalis* Curtis, 1834. Redescribed as *A. albiterminata.*

**delicatula* (Tillyard), 1935. To *Atalonella.* Type: British Museum.

**furcifera* (Eaton), 1871, in *Leptophlebia.* To *Atalophlebia* Eaton, 1888, *Deleatidium* Ulmer, 1938. Type: National Museum of Victoria.

**fusca* (Ulmer), 1919. To *Atalonella* Needham and Murphy, 1924.

**fuscula* (Tillyard), 1935. To *Atalonella.* Type: British Museum.

hudsoni Tillyard, 1935. Type: Unknown.

ida Tillyard, 1935. Type: British Museum.

incerta Harker, 1950. Type: Australian Museum.

inconspicua (Eaton), 1871. In *Leptophlebia.* To *Atalophlebia* Eaton, 1888. Type: Hope Museum, Oxford.

kala sp. n. Type: British Museum.

kokunia sp. n. Type: British Museum.

longicaudata Harker, 1950. Type: Australian Museum.

maculosa Harker, 1950. Type: Australian Museum.

**lucida* (Ulmer), 1919. To *Atalonella.* Type: Stockholm Museum.

marowana Harker, 1950. Type: Australian Museum.

miunga sp. n. Type: British Museum.

**parva* (Harker), 1950. To *Atalonella.* Type: Australian Museum.

pierda sp. n. Type: British Museum.

**sexfasciata* (Ulmer), 1917. To *Atalomicria.* Type: Stockholm Museum.

**simillima* (Ulmer), 1919. To *Atalonella.* Type: Stockholm Museum.

**strigata* (Eaton), 1871, in *Leptophlebia.* To *Deleatidium* Ulmer, 1920 (referred to as *D. strigatum*). Type: McLachlan Museum (?).

superba Tillyard, 1935. Type: British Museum.

tuhla sp. n. Type: British Museum.

**uncinata* (Ulmer), 1917. To *Atalomicria.* Type: Stockholm Museum.

Deleatidium Eaton, 1899. Type-species *D. lilli* Eaton.

decipiens sp. n. Type: British Museum.

furcifera (Eaton), 1871, in *Leptophlebia.* To *Atalophlebia* Eaton, 1888, *Deleatidium* Ulmer, 1938. Type: National Museum of Victoria.

mjobergi (Ulmer), 1917, in *Euphyurus.* To *Deleatidium* Ulmer, 1920.

nanatum sp. n. Type: British Museum.

pusillum sp. n. Type: British Museum.

strigata (Eaton), 1871, in *Leptophlebia.* To *Deleatidium* Ulmer, 1920. Synonym: *Euphyurus bicornis* Ulmer,.

unguicularis (Ulmer), 1916, in *Euphyurus.* To *Deleatidium* Ulmer, 1920. Type: Stockholm Museum.

Deleatidium (*Atalophlebiodes*) Phillips, 1930.

annulatum Harker, 1950. Type: Australian Museum.

bundutum sp. n. Type: British Museum.

crassa (Harker), 1950 in *Leptophlebia.* Type: Australian Museum. **Comb. nov.**

Jappa gen. n. Type-species *J. kutera.*
kutera sp. n. Type: British Museum.
tristis sp. n. Type: British Museum.

Kirrara gen. n. Type-species *K. procera.*
amenia sp. n. Type: British Museum.
procera sp. n. Type: British Museum.

BAETIDAE.

Baetis Leach, 1815, Type-species *B. bioculatis* Linn.
**australasica* (Pictet), 1843. To *Atalophlebia.* Type: Unknown.
baddamsae Harker, 1950. Type: Australian Museum.
confluens Harker, 1950. Type: Australian Museum.
**costalis* (Burmeister), 1839. Homonym. Removed to *Atalophlebia albiterminata.*
frater Tillyard, 1935. Type: British Museum.
sogeriensis sp. n. Type: British Museum.
soror Ulmer, 1908. Type: Stockholm Museum.

Cloeon Leach, 1815. Type-species *C. dipterum* (Linn.).
fluviatile Ulmer, 1919. Type: Stockholm Museum.
tasmaniae Tillyard, 1935. Type: British Museum.
virens Klap., 1905. Synonym: *C. viridis* Ulmer, 1916; Tillyard, 1935.

Pseudocloeon Klap., 1905. Type-species *P. kraepelini.*
kraepelini Klap. Type: ?

CAENIDAE.

Caenis Stephen, 1835. Type-species *C. macrura* Steph.
**scotti* Tillyard, 1936. Hononym: = *tillyardi.*
tillyardi Lestage, 1938, for *scotti.*

Tasmanocaenis Lestage, 1930. Type-species *T. tonnoiri*, Lest.
tonnoiri Lestage, 1930. Type: ?

SIPHLONURIDAE.

Ameletoides Tillyard, 1933. Type-species *A. lacus-albinae* Till.
lacus-albinae Tillyard, 1933. Type: ?

Coloburiscoides Lestage, 1935. Type-species *C. giganteus* (Tillyard).
giganteus (Tillyard), 1933 in *Coloburiscus.* Type: C.S.R.I.O., Canberra.
munionga (Tillyard), 1933 in *Coloburiscus.* Type: C.S.I.R.O., Canberra.

Coloburiscus Eaton, 1868, as *Coloburus*, preoccupied name, changed Eaton, 1888. Type-species *C. humeralis* (Walker).
haleuticus Eaton, 1871. Type: National Museum of Victoria.

Mirawara gen. n. Type-species *M. aapta.*
  aapta sp. n. Type: British Museum.

Tasmanophlebia Tillyard, 1921. Type-species *T. lacustris* Till.
  lacustris Tillyard, 1921. Type: British Museum.
Tasmanophlebiodes Lestage, 1935. No type-species designated.
  laeus-coerulei (Tillyard), 1921, in *Tasmanophlebia.* Type: British Museum.
  nigrescens (Tillyard), 1933. Type: British Museum.

Heptageniidae.

Atopopus Eaton, 1881. Type-species *A. tarsalis* Eaton.
  spadix Harker, 1950. Type: Australian Museum.

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Vol. 105. Part 13. Pp. 269–314. 3 plates. 30th July, 1954

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

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THE COMMUNITY OF INSECTS IN A PATCH OF WOODLAND MUD.

By G. Crisp, Ph.D., F.R.E.S., and Ll. Lloyd, D.Sc., F.R.E.S.
(*University of Leeds*).

Manuscript received 31st August, 1953.
(Read 4th November, 1953.)

With 3 plates.

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INTRODUCTION.

THIS work is a development from that of Lloyd and his pupils (Lloyd *et al.*, 1940) on the fauna of sewage purification filters. This fauna is composed mainly of a few species of worms and insects (chiefly Chironomidae and Psychodidae) which, because of the rich medium and the specialised environment, abound in enormous numbers that can be assessed with fair accuracy. It was therefore possible to contrast the effects of interspecific and intraspecific competition and to show how species pressure moulded the seasonal rhythm of the various insects from the patterns that their climatic responses alone would produce (Lloyd, 1943, 1945). The same flies were found also breeding in a mud-flat in the bed of a slightly contaminated stream far from a sewage works, but here they were mingled with many other species of Chironomidae and Psychodidae as well as a prevalence of Tipulidae and Ceratopogonidae which are very rare or, more usually, absent under filter conditions (Lloyd, 1944). Much work has been done on individual mud-breeding insects but no study of the mud fauna as a community of larvae is recorded and it is as an introduction to such a study that this paper is offered.

The mud flat where Lloyd (1944) made his first observations lay in the bed of the Gledhow Valley Brook and in summer some 40 per cent. of the emerging flies were of the sewage species. Unfortunately in the intervening years this bank had further silted up and had been invaded by herbs and shrubs so that the wet portion was reduced to a narrow margin. The work was therefore transferred to two small areas of permanent mud in Roundhay Park, Leeds, where also the sewage species were known to be breeding, though in lesser proportion than in the Gledhow flat.

The Roundhay mud flats are in a rather densely wooded glade which is traversed by a small brook. Seepages on one side cause two delta-like areas of mud each with three drainage lines, always wet, but so choked that there is no perceptible trickle of water. From leaf fall to early summer a blanket of leaves conserves the moisture in the surrounding mud but at other times this is more dependent on weather conditions. Sunlight strikes it only in dappled patches. The two wet areas are about fifty yards apart and between them is an embankment cut by a pipe for the main stream. The subsoil is a stiff clay and the black mud is about half an inch deep on the general surface and two to three inches deep in the lines of seepage. It contains many small stones and grains of sand, fragments of wood, twigs and leaves in all stages of decay. Analyses of the mud at many points showed an average of 63 per cent. moisture with a range of 37–82 per cent., while the combustible dry solids averaged 18 per cent. with a range of 11–27 per cent. The upper flat has an area of 130 and the lower one 70 sq. yds. Both flats lie on a slight slope which prevents complete submergence even in the heaviest rains but these tend to drift the mud towards the main stream and so keep the mud layer thin. The brook has a well-cut bed in the clay and, as we are very near its source, only exceptional downpours cause it to overflow. When this occurs the adjoining mud is scoured down to the clay for the width of a foot or so.

Leaf fall covers the mud completely to a depth of one to three inches and is almost wholly absorbed by the following summer. The vegetation bordering the flat may have important effects on the mud fauna for some larvae prefer the dead leaves of one species of tree to another. For instance, soft leaves, like oak and sycamore, are eaten in preference to tough evergreen leaves such as holly. The distribution of some mud-dwelling larvae of Syrphidae is determined by the qualities of the surrounding vegetation to which the adults are specialised (Diver, 1944). The upper flat is bordered by sycamore but close by are beech and birch with a stand of oaks, the leaves of which drift onto the mud. The lower flat is similarly provided but with the addition of ash. The undergrowth consists of holly and some rhododendrons, the former affording the species of *Molophilus* their favourite resting and dancing places. A broad strip alongside the brook is kept cleared as a woodland path but up the glade sides, away from the wet areas, these bushes form extensive thickets.

The glade is too shady to permit of much herbaceous growth but downstream from each flat there is a bed of garlic and above the mud, on the well-drained ground free from thicket, *Cercaea lutetiana* abounds. The lower flat has a short-lived cover of Celandine, the bulbils of which appear in every sample of mud. In 1951 it began to grow in February, the leaves opened in March, the flowers in April and by mid July the entire growth had collapsed and rotted. This food supply, well apart from the woodland leaf fall, is not shared by the upper flat which is void of vegetation apart from a little moss, *Mnium hornum*, infrequent on the sides of stones and twigs, and *Brachythecium rutabulum* in isolated places. There are no extensive growths of algae on the mud, but these, as well as fungi and abundant diatoms, are sometimes seen in the gut contents of larvae.

As the mud flats are in a public place the methods of insect trapping by trays and jars as used on the filters could not be employed. The main methods of study involved : (1) Tubing the insects on the surrounding trees and vegetation (p. 274). (2) Laboratory breeding from bulk samples of mud (p. 275). (3) Collection of early stages by flotation of the mud (p. 277). (4) Rearing larvae and pupae so obtained in isolation (p. 276). The insects encountered fall chiefly into the four families: Tipulidae, Chironomidae, Psychodidae and Ceratopogonidae and a formal list of these is given on p. 272. F following the insect name indicates that it was taken free and the months of capture are given ; B indicates that the insect was reared from mud in bulk ; L indicates that it was reared in isolation so that the larva, or in a few cases only the pupa, was ascertained. Reference to larvae not associated with the imago is also made.

The large number of preparations required called for a very rapid method of mounting and de Faur gum chloral mountant was almost always used. It is a peculiarity of aquatic larvae that they are difficult to wet, but de Faur medium answers best with living material. Therefore the procedure was to wet the insect in 70 per cent. or even 90 per cent. alcohol and quickly drop it to 30 per cent. before transferring it to the slide. A mount made direct from 70–90 per cent. alcohol becomes opaque after the initial clearing. The heads of the Tipulid larvae were pulled out of the thorax, turned ventral side upwards and slightly dissected to reveal the mouthparts. When a view of a truncated spiracular disc was required it was cut off as shortly as possible and it was then placed in a tiny drop of mountant on a coverslip so as to give the posterior view when the slip was inverted onto the large drop holding the larvae. The smaller heads are also more conveniently dealt with in a coverslip droplet. A ventral view of the heads of Chironomid larvae is needed to expose the hypostome and when these would not lie well because of convexity of the capsule they were dealt with similarly. The rapid setting in the droplet usually prevents them from rolling when the mount is completed.

In the larvae of *Pericoma* the arrangement of setae on the dorsal plates is required and as these are dark on a dark background, and the larvae clear poorly in the mount, there is a difficulty. Treatment with sodium hydroxide, with or without bleaching, was not successful in our hands and is a delaying process. When the larvae are cut across, pressed between two slides, dipped into boiling water for a moment, and then mounted, the required features are generally revealed. Ten or more larvae can be dealt with in one operation.

In the later stages of the work it was desired to collect information about the food of the larvae and, as stomach contents are not always recognisable in whole mounts, the stomach contents were often pressed out and slightly teased apart in mounting.

FORMAL LIST OF INSECTS.

In the following list only the more prevalent families are given, others being mentioned in the body of the paper: B, bred from mud in bulk; L, bred in isolation; F, taken free and months of capture. The last, of course, are not certainly breeding in the mud.

Tipulidae.

Tipulinae.

Tipula oleracea L. (F.9).
T. paludosa Meig. (F.9).
T. fulvipennis Degeer (B.F.9).
T. rufina Meig. (B.F.4–9).
T. signata Staeger (F.9–10).
T. irrorata Macq. (F.9–10).
T. maxima Poda (B.L.F.9–10).
Nephrotoma flavipalpus Meig. (F.7–8).
N. quadrifaria Meig. (F.7–8).

Limoniinae.

Tribe Limoniini.

Limonia flavipes Fabr. (F.9).
L. nubeculosa Meig. (B.L.F.4–7, 9–10).
Dicranomyia chorea Meig. (F.6–10).
D. fusca Meig. (F.7–10).
D. modesta Meig. (F.10).
Rhipidia maculata Meig. (F.6).

2 species of larvae of the tribe not identified.

Tribe Pediciini.

Crunobia littoralis Meig. (F.9).
Dicranota bimaculata Zett. (B.L.F. 5–6).
Pedicia rivosa L. (L.F.6–8).
Tricyphona sp. (identified by larva).

Tribe Hexatomini.

Austrolimnophila ochracea Meig. (F.8).
Oxydiscus senilis Haliday (B.L.F.3–6).
O. sp. (identified by larva).
Epiphragma sp.? (tentative by larva).
Limnophila (*s. lat.*).
L. (*Phylidorea*) *fulvonervosa* Schummel (B.L.F.7).
L. (*Elaeophila*) *submarmorata* Verr. (B.L.F.7–8).
L. (*Pseudolimnophila*) *lucorum* Meig. (B.L.).
L. (*Pilaria*) *discicollis* Meig. (B.F.7–9).
L. (*P.*) *nemoralis* Meig. (B.F.6–7).

The larvae of the two *Pilaria spp.* have been collected but not reared in isolation.

Tribe Eriopterini.

Lipsothrix remota Walker (F.7).
Gonomyia (*s. lat.*)
G. (*Gonomyia*) *lucidula* de Meij. (L.F. 7–9).
Gonomyia sp. (identified by larva).
Cheilotrichia (*s. lat.*)
C. (*Platytoma*) *cinerascens* Meig. (B.L.F. 5–7, 9–10).
Erioptera (*s. lat.*)
E. (*Erioptera*) *lutea* var. *taenionota* Meig. (B.L.F.6–10).
E. (*Ilysia*) *maculata* Meig. (B.L.F.6–10).
E. (*I.*) *occoetata* Edw. (B.F.7).
E. (*I.*) *vicina* Tonn. (F.9).
Ormosia (*s. lat.*)
O. (*Ormosia*) *nodulosa* Macq. (F.5–10).
O. (*O.*) *albitibia* Edw. (F.7, 9).
O. (*Rhypholophus*) *haemorrhoidalis* Zett. (L.F.9–10).
O. (*R.*) *varia* Meig. (F.10).
1 species of larva, probably *Ormosia.*
Molophilus griseus Meig. (B.L.).
M. undulatus Tonn. (B.L.F.9–10).
M. curvatus Tonn. (B.L.F.6–10).
M. serpentiger Edw. (L.F.6).
M. cinereifrons de Meij. (B.F.7–10).
M. ochraceus Meig. (B.F.7–10).
M. appendiculatus Staeger (F.8–9).

Chironomidae.

Tanypodinae.

Pentaneura monilis L. (F.5).
P. phatta Egger (F.5).
P. melanops Meig. (B.L.F.8).
P. binotata Meig. (B.L.).
Pentaneura sp. (larva not associated).
Anatopynia notata Meig. (L.F.9).
Procladius choreus Meig. (F.9).

Orthocladiinae and Diamesinae.

Prodiamesa olivacea Meig. (L.F.5–10).
Brillia modesta Meig. (B.L.F.3–4, 10).
B. longifurca Kieff. (F.7, larva identified but not reared).
Metriocnemus (*s. lat.*)
M. (*Metriocnemus*) *hygropetricus* Kieff. (*longitarsus* Goet.) (B.L.F.4).
M. (*M.*) *hirticollis* Staeg. (B.L.F.10).
M. (*M.*) *gracei* Edw. (L.F.10–11).
M. (*Paraphaenocladius*) *impensus* Walk. (B.L.F.7–9).
M. (*Parametriocnemus*) *stylatus* Kieff. (B.L.F.7–8).
Trichocladius foveatus Edw. (B.L.F. 2–10).
T. dispar Goet. uncertain (B.L.).
Diplocladius cultriger Kieff. (F.10–11).
Orthocladius apicalis Kieff. (F.8, 11).
O. piger Goet. (B.L.F.1–3).
Limnophyes minimus Meig. (B.F.8).
L. prolongatus Kieff. (B.L.F.6).
L. pusillus Eat. (B.F.2).
L. sp. incog. near *pusillus* (B.L.F.3–4).
Corynoneura scutellata Winn. (L.F. 10–11).
C. sp. incog. (F.10–11).

4 following were identified by larvae :–

Pseudorthocladius sp.
Pseudosmittia ?trilobata Edw.
Phaenocladius near *aquatilis* Goet.
Orthocladius sp. Edwards' Group B = *Bryophaenocladius* Th.

5 other species of larvae of this sub-family were not more closely identified.

Chironominae. *Chironomus s. lat.*

Chironomus plumosus L. (F.7–8).
C. riparius Meig. (F.8–9).
C. (*Paratendipes*) *albimanus* Meig. (F.9).
C. (*Microtendipes*) *nitidus* Meig. (B.F.9).
C. (*Polypedilum*) *albicornis* Meig. (B.F. 9).
C. (*P.*) *nubeculosus* Meig. (F.7–8).
3 species of larvae of *Chironomus* (*s. lat.*) were not associated.
Tanytarsus s. lat.
T. (*Microspectra*) *subviridis* Goet. (B.L.F.4, 10).
T. (*Stempellina*) *bausei* Lieff. (B.L.).

Ceratopogonidae

Dasyhelia sp. incog. (B.L.F.6).
Culicoides obsoletus Meig. (B.L.F.5–8, 10).
C. vexans Staeg. (B.L.).
C. pulicaris L. (B.L.).
C. odibilis Aust. (B.F.10).
C. impunctatus Goet. (B.F.8).
Stilobezzia gracilis Hall. (B.L.).
Palpomyia flavipes Meig. (B.L.).
P. serripes Meig. (B).
P. quadrispinosa Goet. (B.L.).
P. nemorivaga Goet. (B.).

Psychodidae

Pericoma fusca Macq. (B.L.F.6–7, 9).
P. fuliginosa Meig. (B.L.F.4–6, 8–10).
P. gracilis Eat. (Taken mixed with *P. crispi.*)
P. crispi Freeman (B.L.F.8–10).
P. pilularia Tonn. (B.L.F.10).
P. trivialis Eat. (B.L.F.4–10).
P. canescens Meig. (B.L.F.4–10).
P. neglecta Eat. (L.).
P. blandula Eat. (B.L.F.7–8).
P. pulchra Eat. (B.L.F.4–6).
P. avicularia Tonn. (B.).
Telmatoscopus tristis Meig. (B.F.6).
T. soleatus Walk. (B.L.F.6).
Psychoda severini parthenogenetica Tonn. (B.L.F.6–7, 10).
P. gemina Eat. (B.F.7).
P. cinerea Banks (B.L.F.6–7, 10–11).
P. albipennis Tonn. (F.7, 10).
P. phalaenoides L. (F.7–10).
P. alternata Say (F.7).
P. setigera Tonn. (B.L.F.10).

FREE COLLECTING.

The association of insects over the mud flat was studied by routine observations of the forms resting on the surrounding tree trunks and vegetation, representative samples being collected chiefly by tubing. The species collected and identified in the four principal families are indicated in the formal list above by F followed by the months of capture. No counts of the collected insects were made as such would be so strongly influenced by habit that a false impression of the composition of the fauna would be gained. The general impression gathered was that the frequency bore a reasonable relationship to larval abundance in the mud in Psychodidae, the commoner Chironomidae and Eriopterini, the first two mainly taken on tree trunks and the last mainly on foliage, especially on holly in the case of *Molophilus*. Tipulinae and Hexatomini seemed scarcer than expected from larval abundance but this could be due partly to the higher resting places, partly to a wider dispersal and, possibly, a generally longer larval life. In Ceratopogonidae *Culicoides spp.* were also scarce in relation to larval abundance and laboratory emergence, probably because of their inconspicuous habit, and neither *Palpomyia* nor *Stilobezzia* were recorded though these are fairly conspicuous flies and species were abundant as larvae and in laboratory breeding.

Of the 93 species recorded as taken free in the formal list, 61 were proved to be breeding in the mud. Of the others some will be mud-breeding forms with larvae undetected, some will be from drier situations and others from nearby waters, the adjoining brook or lake. *Chironomus plumosus* and *C. riparius* were at times very abundant on the trunks but their larvae were not taken. In Culicidae species of *Anopheles*, *Culex*, *Aedes*, *Theobaldia*, *Chaoborus* and *Dixa* were all taken, with some species frequent, but only *Dixa* was represented amongst the larvae. Oviposition of some of these and of the *Chironomus* mentioned in small transient pools on the mud flat is a likelihood with a general failure to survive. Other observations made during these free collections are recorded through the text.

BREEDING FROM MUD IN BULK.

The samples of mud used were obtained by scraping an area about 20 cm. square and they measured about 250 ml. The sample was heaped on a sheet of waterlogged cotton wool spread on a plate and covered by a cylinder 20 cm. tall and 12·5 cm. in diameter. This was closed by a glass plate resting on 4 strips of gummed paper to allow ventilation and reduce dewing. Under these conditions the mud did not become corrupt. It was moistened as required and kept under observation for at least a month and then in most cases it was floated out to recover immature insects. The emerging insects were abstracted at intervals of one to three days according to rate of emergence. This was effected in a large perspex chamber by removing the cover and taking the insects into a tube onto chloroformed wool. The cylinders were kept in the laboratory which was always at summer temperature and this may, of course, have been deleterious to insects with a strict seasonal behaviour. On the other hand, had they been kept at natural temperatures emergence would have virtually ceased for five months of the year.

This method of assessment of the fauna, like the last, is not uniformly satisfactory. Psychodidae, species of *Metriocnemus* (*s. lat.*), *Limnophyes spp.*, most of the Eriopterine Tipulidae and Ceratopogonidae are well suited by the conditions but this is not so of the Hexatomine Tipulidae and Chironominae. Their emergence in the cylinders was far below that expected by the abundance of their larvae in the mud. For instance the larvae of *Oxydiscus senilis* and *Phylidorea fulvonervosa* have appeared in most of the flotation samples, and often abundantly, but the former has emerged only once and the latter only 10 times. In *Molophilus* the emergence numbers have been: *M. ochraceus* 116, *M. undulatus* 31, *M. curvatus* 18, *M. griseus* 12, *M. cinereifrons* 5, *M. appendiculatus* 0, and *M. serpentiger* 0. The two last, and especially *M. griseus*, have been often bred in vials from larvae isolated by flotation, so it is reasonable to suppose that their larvae were present in numbers in the cylinders but have not found conditions there congenial. Similarly the larvae of *Brillia modesta*, *Trichocladius foveatus*, *Microspectra subviridis* and *Orthocladius piger* have all been abundant seasonally in flotations but cylinder breeding from equivalent bulk samples has yielded very few of these.

The artificially high temperature, about 64° F., has hastened some life cycles but left others apparently unaffected. For instance *Limonia nubeculosa* emerged in January but was not taken free till April. *Phylidorea fulvonervosa* emerged in January and February but was not taken free until July. About 90 *Erioptera lutea* emerged from October to March, and *Molophilus ochraceus* and *M. undulatus* bred out in relatively large numbers from November to March. All these are out of season. *M. cinereifrons* emerged in June and July only, *M. curvatus* in May and June only, *M. griseus*, the larva of which was ascertained and known to be abundant throughout the year, emerged only in July and August. These three species coincide with their capture in the field.

In regard to *Pericoma*, the abundant *P. blandula* has agreed with its natural summer incidence but the other common species have emerged in the laboratory throughout the year with some depression in winter. *P. trivialis* with 97 flies and *P. fusca* with 86 flies from 27 samples between November and February, though in the field the former did not appear till April and the latter till June, show a strong response to heat. In Ceratopogonidae species which show a similar response are *Culicoides vexans*, *Palpomyia flavipes* and *P. quadrispinosa*. *Stilobezzia gracilis*, however, was restricted to May to July when the flies emerged freely in the cylinders and the pupae were abundant in flotations.

The first flies to emerge from a sample were almost always one or more of the abundant species of *Limnophyes*. In summer this occurred a day or so after the sample was taken but in winter after a week or more. This phase continued for several days and then stopped abruptly. Flotations show *Limnophyes* larvae of all sizes though the pupae which are in dense cocoons were not recorded and it is probable that during the cold months mature larvae are awaiting the stimulus of warmth to pupate. The younger larvae probably die, for flotation after the stopping of the culture, usually after about a month, never revealed any larvae of Chironomidae. Tipulidae, Ceratopogonidae and *Pericoma* continued to emerge long after the Chironomidae had ceased. When samples had been kept for more than six months and then floated some Tipulid larvae were usually recovered and emerged as flies after a further period of isolation. This was the case with *Molophilus undulatus* and *M. griseus*.

The chief value of the bulk breeding method is that it reveals with certainty a large proportion of the association of insects taken over the mud flat as mud-dwelling. The flies of the four prevailing families of the Nematocera which emerged in the cylinders are indicated by B in the formal list above. This shows that of 93 species recorded from the free collecting, 52 species emerged in the cylinders while 17 species emerged under these conditions but were not encountered free. That is 69 mud-breeding forms in these families were ascertained for the site but it is not supposed that the list is by any means complete.

Breeding in Isolation.

In order to associate the early stages with the adults it is usually necessary to rear them in isolation under conditions that allow of the recovery of the exuviae. Larvae in which approach to maturity was indicated by an empty gut and swollen thorax were chosen when possible. They were isolated in tubes on wetted cotton wool and confined by a cork with a deep notch holding a pledget of wool. This artificial medium has advantages over mud or decayed leaves, which were sometimes used, because the exuviae are conspicuous in it, it is free from foreign organisms and its water content is easily controlled by a teated pipette. Like the sewage insects the mud dwelling larvae usually seem comfortable in it. Tipulidae rarely leave it, though some *Pericoma* and Chironomidae are apt to climb to the cork and get lost through desiccation. There is also often loss in the pupal stage through moulds. Sphagnum moss proved to be the best of the alternative materials tested.

When immature larvae were set up and feeding was required a small mass of filamentous alga or decayed leaf was generally taken by the gross-feeding forms while the carnivorous Chironomidae and Tipulidae were fed on smaller larvae or small Oligochaete worms, a supply being usually available from the flotations. Later, Dr. Hans Bauer, Max Planck-Institut für Meeresbiologie, has informed us that for years he has used urtica powder (*fol. pulv. urt.*) for rearing crane-flies and that he applied it with success to *Metriocnemus hygropetricus* when in difficulties with a supply of alga for this species.

Flotation Record.

The method of Ladell (1936) somewhat modified was employed. Scrapings of the mud of about 125 ml. were emptied into rectangular glass chambers holding 500 ml. and these were filled with magnesium sulphate solution of S.G. 1·07. After a stirring, larvae and debris surfacing quickly were picked off and gross material such as leaves and stones was shaken, inspected and removed. Stirring was continued until the mud was reduced to a cream-like consistency and surfacing forms were taken off under a reading glass, the lower limit of size being about 1·0–1·5 mm.

Under these conditions free pupae and most larvae surface readily and some tubicolous forms also leave their shelter and float. Those species of *Pericoma* weighted with a coating of mud and some of the tubicolous forms remain at the bottom. When surfacing had ceased the mud was allowed to settle and the supernatant fluid was gently decanted off. The mud was then poured in a very thin layer in a dish 25 × 30 × 4·5 cm. and allowed to stabilise. Many of the unfloated forms then showed their presence either by breaking the surface with respiratory dimples or making tracks as they crept in the smooth mud. These were collected at intervals and placed in a dish of water with the floating forms. The procedure caused no apparent mortality in insects but was deleterious to small Oligochaete worms.

This method of assessing the fauna gives the best indication of the seasonal prevalence and relative abundance but there is the difficulty that the early stages are less well known than the imagines. Larvae and pupae within the genus are commonly extremely similar to one another and, though one or more species in most of the genera of Nematocera have been described, the descriptions are often of generic value only because the slight differences that would serve to distinguish species have not yet been recognised.

In order to surmount this difficulty as far as possible most of the larvae collected by flotation have been mounted and a series of drawings of each distinctive form has been made and serially numbered within the families mainly concerned. As the collection of mounts and drawings accumulated it became easier to sort the great number of larvae encountered. It was not possible to deal as fully with the pupae of Nematocera, or with the relatively small number of the higher Diptera encountered. Where possible the larvae and pupae were bred through and the adults submitted to Mr. Paul Freeman for identification. Others were identified, generally only to the genus, from published description. Where neither was achieved the forms remain under their numbers. In the coding, in Tipulidae especially, juvenile and later larval stages often received separate numbers, while some cases of duplication were later corrected. For these reasons the code numbers do not now run consecutively.

342 samples were floated from November, 1950, to April, 1952. For the first nine months samples of 125 ml. were taken but later 250 ml. were used.

As these were floated in two equal parts the whole series is equated to 125 ml. The results in summary in Table I give a general idea of the variety of the forms and abundance of individuals encountered. The numbers of species taken in the samples were higher, and sometimes much higher, than the number of "forms" recorded because in some of the prevalent genera the larvae and pupae were not distinguished *inter se* to the end of the work. This applies particularly to *Molophilus*, *Limnophyes* and to all genera of Ceratopogonidae encountered. For though many of these were bred through in isolation and ascertained exuviae obtained it was not possible to match the floated insects against these. Dr. van Emden has informed us that he still faces this difficulty with the larvae of *Tipula*.

TABLE I.—*Summary of Flotation Record.*

		No. of forms.			No. of individuals.		
1950.	No. of samples.	Lowest.	Highest.	Average.	Lowest.	Highest.	Average.
November	4	8	16	11·3	26	66	39·2
December	5	11	18	12·8	28	79	58·0
1951.							
January	11	7	17	10·4	26	224	66·9
February	20	6	21	10·8	12	173	58·6
March	13	5	19	13·5	23	93	50·1
April	13	6	16	10·0	22	82	49·9
May	24	4	17	10·2	9	64	29·9
June	12	5	13	8·7	12	68	32·5
July	13	5	22	11·3	15	88	34·1
August	17	4	11	7·1	4	68	17·4
September	24	3	16	11·0	5	27	14·7
October	34	3	19	11·9	5	63	25·1
November	44	7	23	13·3	10	184	35·1
December	12	10	21	16·1	11	63	37·7
1952.							
January	24	5	20	13·1	4	88	28·0
February	32	6	18	12·8	11	86	30·9
March	28	6	19	11·6	6	69	31·9
April	12	9	18	11·2	12	47	23·4

"Forms" are mainly species but several groups of closely similar species are recorded as single forms.

The samples measured about 125 ml. of mud.

The table covers all insects except Collembola, which were ignored. Larvae under 1·0 mm. in length and no doubt many rather larger would be missed. 11,573 were recorded, averaging 34 per sample, and of these 99·4 per cent. were Diptera, 97·7 per cent. Nematocera, while there were only 44 beetles and their larvae. The figures are referred to again in the Discussion (p. 304) while the Nematocera are dealt with in detail under their families. The yield was at its highest in mid-winter and at its lowest in August–September. This is what could be expected in a temperate climate where many of the Nematocera are bivoltine, the second flight, and so a minimum of larvae and pupae, being at the end of summer.

In winter the freezing of the mud does not seem to have any effect on the life within. On several occasions the mud was frozen solidly and samples had to be chopped out. Such a sample was taken on 29.i.52 and gave 59 larvae as follows: *Molophilus* complex 2, *Rhypholophus haemorrhoidalis* 3, *Pericoma crispi* 1, *P. trivialis* 1, *P. fuliginosa* 1, *Brillia modesta* 11, *Orthocladius piger* 9, *Limnophyes* complex 12, *Trichocladius foveatus* 1, *Metriocnemus hygropetricus* 2, *Paraphaenocladius impensus* 9, *Parametriocnemus stylatus* 3, *Microspectra subviridis* 3, *Pentaneura binotata* 1. This list will serve as a typical yield from a sample while other instances are recorded by Crisp (1952).

Cameron (1913) states that ground beetles and surface larvae which hibernate generally descend deep into the subsoil in order to avoid the frost-bound surface. In mud, which freezes solidly, this is apparently not the case, at least in our climate, since frozen samples showed such a large fauna. Further, at the beginning of the work early in the winter samples were taken from a depth of 2–3 inches as well as from the surface layers. Although the latter was then productive the fauna at a depth of two inches was so sparse that the deeper samples were discontinued in January. It consisted almost entirely of Ceratopogonidae and Tipulidae of the *Molophilus* complex. Thus in nine deep samples the total of individuals was only 42, comprising 20 Ceratopogonidae, 18 Tipulidae and 4 Chironomidae. Below the shallow rich mud, however, the subsoil is tenacious clay. Where black mud is deep a different result might be obtained.

Early summer samples are characterised by the large number of pupae which they contain. For instance, the sample collected 19.vi.51 yielded: larvae, *Molophilus* complex 4, *Limonia nubeculosa* 1, *Pericoma fuliginosa* 3, and pupae, *Stilobezzia gracilis* 41, *Palpomyia flavipes* 9, *P. quadrispinosa* 7, *Culicoides vexans* 3, *Pericoma fuliginosa* 3, and *P. trivialis* 4.

Yields from samples taken at the same spot varied greatly at short intervals. For instance, a sample taken on 19.iv.51 yielded 24 Chironomids in 2 species while the sample at the spot a week later gave 60 Chironomids in 8 species. Great local densities of a species were not uncommon; e.g., that of *S. gracilis* just quoted. A sample on 19.i.51 held more than 200 *Microspectra subviridis*, the mud being almost agglutinated by the long rambling tubes. The sample on 4.iii.52 contained 52 *Paraphaenocladius impensus*. On several occasions over 50 *Molophilus* complex occurred and similar quite local densities of the commoner species of *Pericoma* were encountered. These events suggest that broods from successful local ovipositions have not dispersed far in their larval life.

Larvae of Tipulidae.

These insects form the most prominent component of the mud flat fauna and show in a close association nearly all the remarkable adaptations that have developed in the family, a range of structure that is unequalled in the larvae of any other insect family. Great differences in structure are found in forms whose imaginal characters show close relationship and these involve not only secondary features, such as the respiratory mechanism, but more fundamental structures such as the head capsule. In order to illustrate this, frequent reference will be made to the Hexatomine forms *Pilaria* (*s. str.*), *Pseudolimnophila*, *Oxydiscus* and *Epiphragma*. The first two are subgenera of *Limnophila* which includes also *Phylidorea*, *Elaeophila* and *Limnophila* (*s. str.*). *Pilaria* (*s. str.*) is a very specialised predatory form, *Epiphragma* feeds in decaying wood while *Pseudolimnophila* and *Oxydiscus* are gross feeding forms in the surface of leafy mud, *O. senilis* making also a special selection of thecate rhizopod Protozoa. A general account of the external features and the head is first given. The terminal segment is also discussed in a general way (p. 284). This is followed (p. 285) by a more particular account of the forms encountered, with reference to their respiratory mechanisms, and their abundance as found by flotation. These are dealt with in their tribes and at the end of each tribe is given a note on feeding habits and reference to special features of juvenile larvae where these are known.

Tipulid larvae include both terrestrial and aquatic forms and all live a concealed life in earth, mud, or vegetable matter. In consequence they are neutral in colour, varying from white or yellow to almost black, and with some instances in which the cuticle is transparent, e.g., tube dwelling Limoniini. Though some forms are nearly naked, apart from sensory setae, the majority are clothed in a characteristic dense fur-like vestiture but in *Tipula* the hairs are sparser and of a spiny nature. In many cases creeping welts of spines are developed on the abdominal segments and rarely these are elevated to form pseudopods, e.g. *Dicranota*. In keeping with the burrowing life they are nearly all cylindrical and not markedly retractile, but Tipulinae, *Oxydiscus* and *Pseudolimnophila* and a few others have a great power of retraction in a crumpled manner. This power is probably connected with frequent surface excursions. The head is retracted into the thorax and the respiration is metapneustic, the combination of these two characters distinguishing them from other nematocerous larvae.

The connection between head and body is made by the union of a soft fold of the prothorax with the head capsule just behind the mouth and this affords to the head much the same power of movement as a normal neck gives and, in addition, a piston-like thrust. The generalised head capsule is formed of three rigid plates, a fronto-clypeus and two side pieces or lateralia. The latter are shaped like the valves of a mussel (Alexander, 1920) and this description is apt because they commonly show concentric striations like growth lines. The lateralia meet in the midventral line anteriorly and diverge behind. On the dorsal surface the lateralia and the frontoclypeus meet in front and their fusion runs backwards for a variable distance till they also diverge. Thus there are three incisions in the rigid head capsule, a deep mid-ventral incision and two dorsolateral incisions of varying depth, shallow in Pediciini, deeper in Limoniini and Tipulinae, and extending almost the length of the capsule in the specialised Hexatomini and Eriopterini. In the generalised head the lateralia at their junction are very rigid and the free edge develops a row of saw-like teeth. This structure is the "mentum" of Alexander (1920) but is now more strictly called the "hypostome" (Anthon, 1943, Hennig, 1950). The structure is universal in Chironomid larvae.

There is a tendency for the rigidity of the three main sclerites to concentrate in their margins with the interior of the plates paler and more flexible. This is best seen in younger larvae and especially in the early instars of *Pseudolimnophila* in which the margins are jet black (fig. 13). These black bands run forwards along the edges of the frontoclypeus nearly to the front of the head capsule, loop backwards as the edges of the lateralia, loop again forwards round the hind sides of the head and, now ventral, converge to the mouth where each expands into a toothed black plate which together form the hypostome. In the final instar the whole of the plates becomes jet black and rigid. This form is very interesting because a break in the loops at the posterior ends of the lateralia would give the condition found in Eriopterini and most Hexatomini (fig. 14). In these the rigid part of the head capsule is reduced to six rods, two dorsal, two lateral and two ventral. These rods are narrow anteriorly but flange out more or less behind in a spatulate manner. In the last instar larva of *Pilaria* (*s. str.*) a smoky-coloured membrane extends between the dorsal rods on the one hand and from the lateral to the ventral rods on the other hand, but usually there is no sclerotisation evident in these areas.

These specialised head capsules are termed "dissected" as opposed to the "massive" generalised type. They are very flexible, for the rods can work to some degree like the ribs of an umbrella. This is undoubtedly an adaptation for rapid burrowing for such a head can be pushed into very narrow crevices. Certain other characters develop with it. The thoracic segments and the penultimate segments of the abdomen have the capacity for enduring expansion thus giving some anchorage in semifluid mud. The terminal respiratory segment is narrowed in its base, which can be retracted into the penultimate segment during progression, with improvement of the stream-line. A pair of static organs (p. 284) is present on the terminal segment and these are known to be concerned with orientation.

The support of the mouthparts is of necessity modified in the dissected head. The dorsal and lateral rods end some distance behind the mandible base, sometimes with complete fusion (e.g. *Pilaria* (*s. str.*)), and sometimes with a suture (Eriopterini). The ventral rods end independently. From the union of dorsal and lateral rods in Eriopterini a sturdy rod runs forwards and the ends of the pair are joined by a strong bridge just behind the base of the labrum. This affords a fulcrum for the upper mouthparts. This dorsal bridge is represented in *Phylidorea*, *Elaeophila* and *Pilaria nemoralis* but it is incomplete in the middle line, allowing the wide gape required by the mandibles of these predatory forms, but it is not present in *Pilaria* (*s. str.*). In this larva the dorsal and lateral sclerites fuse in a jet black knob and from this a curious sclerite runs forwards to the mandible base. It is shaped like a narrow V with rigid arms connected by a weaker plate of chitin. The exact detail has not been followed but the ends of these divergent arms seem to afford a flexible articulation for the mandible and seem designed to aid in the extreme mobility required by the method of feeding of this larva as explained below.

The antennae are inserted close to the mandibles and are composed of one, usually, or two joints with a terminal papilla and one or two setae. In many Limoniini the apical papilla is button-like and often reduced. In the predatory *Limnophila* (*s. lat.*) it is elongated and spirally sculptured, *Pilaria* (*s. str.*) being an extreme case with the papilla longer than the basal joint. *Pseudolimnophila* agrees with other *Limnophila* in antenna structure. *Oxydiscus* has an elaborate group of sensillae at the antenna end in addition to the usual papilla. In Eriopterini the papilla is often markedly asymmetrical.

Labrum and epipharynx are well developed in all the larvae and the latter bears numerous sensillae and is often brush-like. The brush is strongly developed in the gross-feeding Eriopterini.

Two main forms of mandible occur, a broad massive type in gross-feeding and phytophagous forms and a hook type in predatory species. The former has usually a strong row of teeth along the ventral edge and a weaker row along the dorsal edge with two teeth at the tip. There is a well developed prosthecal tuft of hairs and one or two setae on the outer edge near the base. This generalised type is found in some or all the members of the major groups except in Pediciini, but the number of teeth is often reduced, especially in Tipulinae, some of which have only three teeth in all. This reduction is accompanied by narrowing and elongation of the mandible and is probably an adaptation for a diet of fresh leaves. By contrast, in the saprophagous Eriopterini the mandibles are concave and the teeth form an even frill round the edge. The hook type of mandible is seen in Pediciini where there is a strong terminal point followed by a saw-like cutting edge and vestiges of the dorsal row of teeth. It is found also in the predatory Hexatomini where it is more specialised with a long terminal point and a cluster of weaker teeth about half-way down the blade. In *Pilaria* (*s. str.*) and the Nearctic *Ulomorpha* an extra joint develops so that the mandible can close on itself like a pocket knife meeting a rod on the prostheca in a somewhat chelate manner. The basal portion of the mandible is rigid along its anterior and posterior edges but membranous on its upper and lower faces. The extra joint, together with the flexible base and the special union between the base and the head rods mentioned above, allows the organ to sweep through a full half circle, gripping the worms on which the larva feeds and pushing them far down the gullet in a succession of thrusts. The mandibles of *Pseudolimnophila*, *Oxydiscus* and *Epiphragma* are of the generalised type, broad and with many teeth.

The generalised maxilla, found in most gross-feeding forms, is composed of two humpy lobes beset with comb-like hairs and spines and with a reduced palp. In all the predatory forms it is elongated with a tendency to reduction of the inner lobe and with no separate palp. The extreme condition is found in such forms as *Elaeophila* (fig. 16) and *Phylidorea* where the outer lobe protrudes even when the head is retracted. It has sclerites in its wall and in part has a vestiture, fur-like as on the body. The inner lobe is reduced to a hump of sensillae about half-way down the stem. Such a development is concerned with the orientation of the prey which is swallowed whole (fig. 15). In *Pilaria* (*s. str.*) the maxilla has a conical furred base which extends into an elongated, but not protruding, lobe, the cuticle being membranous apart from a slender supporting rod. No inner lobe has been detected. In *Pseudolimnophila* the organ is quite exceptional for a gross-feeding form. It is stout, protruding, two jointed, each joint with a ring sclerite, without vestiture, and the inner lobe is a hump of sensillae near the tip. In *Oxydiscus* both lobes are elongated and separate, not protruding, the inner lobe about two-thirds the length of the outer, and there is a patch of fur near the tip of the outer lobe. In Pediciini the organs are also elongated but not protruding and in the three species observed there are three stages in the reduction of the inner lobe, for in *Pedicia rivosa* the two lobes are subequal and separated from the base as in *Oxydiscus ;* in *Dicranota bimaculata* the inner lobe is reduced to a cluster of sensillae near the tip of the outer lobe ; in the third, *Tricyphona sp.* conditions are intermediate between these. In all these forms with elongated maxillae the sensillae at the lobe tips are rich, including plates, papillae and setae. In the wood-eating *Epiphragma* the maxillae are of the generalised humpy type.

The hypopharynx is the most varied structure in the Tipulid head and its strength and armature show that it performs heavy work in the procuring of food. By contrast, the labium is only weakly developed and is in close connection with the hypopharynx (Anthon, 1943). In *Tipula* at the salivary orifice there is a flat plate with five rounded teeth (three only in the early instars observed) and two short arms directed backwards, while above the plate lies a spiny rasping lobe. In Limoniini both above and below the orifice there is a rigid plate with many comb-like teeth. In Pediciini the hypopharynx is a prominent piston-like lobe with strengthened parallel sides and between their tips a crater-like depression which is spiny and flexible and on this lies the orifice.

In the predatory *Limnophila* (*Pilaria* (*s. str.*) and *Ulomorpha* excepted) the hypopharynx (fig. 14) is composed of a middle transverse bar perforated by the orifice and the ends of this are attached to the ventral head rods far back in the head. The attachment is composed of an anterior and posterior sclerite, the former being broad and capable of torsion and the latter more slender. The union between these two can best be likened to that made when a brittle stick is broken with long splintering and then loosely rejoined. In some forms (e.g., *Phylidorea*) the union with the ventral head rod is of a similar nature, for the arm of the hypopharynx splits and one element fuses with the head rod and the other is, presumably, attached to muscle. These joints allow a gentle bending of the whole structure which is highly flexible and forms the " lower jaw " in the snake-like gape when prey is engulfed. The region round the orifice is not beset with spines but just below it is a pair of palp-like sensory organs, probably the labial palps. In *Pilaria* (*s. str.*) there is no sclerite connected with the salivary orifice which lies at the tip of a soft nipple with a weak lobe bearing a few hairs on either side. This form and *Ulomorpha* are unique amongst Tipulid larvae in the absence of any rigidity in the ventral region of the mouth, either in hypopharynx or hypostome, and this lack is no doubt associated with their method of engulfing worms (p. 282).

In the gross-feeding *Pseudolimnophila*, *Oxydiscus* and *Epiphragma* and in Eriopterini the sclerites supporting the hypopharynx are on the same plan as in typical *Limnophila* but the side rods are short and connection with the head capsule is close to the mouth. They all have rasping devices of comb-like spines around the salivary orifice. Alexander (1920) remarks that the hypopharynx in *Adelphomyia* (= *Oxydiscus*) protrudes beyond the other mouthparts and we have seen it in this position but in most of the preparations it lies between and below the bases of the mandibles.

In all the forms with massive head capsules the floor of the mouth is made rigid by the hypostome. This, as explained above, is a toothed prolongation of the lateralia and it is rigidly fused at a middle tooth in Tipulinae, Limoniini and *Epiphragma*. It is sutured in the middle line in *Pseudolimnophila*, sutured or locked together by teeth in Pediciini and composed of two quite separate plates in *Oxydiscus*. It is not present in predatory *Limnophila* and in most Eriopterini but appears again in *Molophilus* where the ventral head rods expand at the tips into hand-like digging plates. These are widely separated and armed with five strong teeth.

The terminal segment in Tipulid larvae carries the two large spiracles surrounded by accessory respiratory structures; it also bears the anal " gills " or papillae, and, in some cases, the statocysts. The last two organs are conveniently discussed in a general way but the respiratory structures are so varied that a more particular account is needed. Advantage is therefore taken of this listing to add notes on identification, frequency in the mud, and habits, where these have been previously recorded, or noted in the present work. The pioneer worker in the subject was Beling (1816-1898), a forester by profession, who published descriptions of 69 species covering most of the genera. His descriptions are very detailed but not illustrated and it will be readily understood that they are mainly of generic value, the knowledge of the species of crane-flies having been extended so enormously since his day. The indispensible work is that of Alexander (1920) from which most of the British genera can be distinguished.

Anal papillae are universally present in Tipulidae and are conspicuous lobes. They number four in all except some Tipulinae where they divide to form six or eight. They are retractile but in the mud dwelling forms never seem to be entirely withdrawn. In Eriopterini they are short and blunt, in Hexatomini long and finger-like, while in Pediciini they are long and tend to be constricted into segments, pronounced in *Pedicia*. *Epiphragma* (our tentative indentification) also shows this condition. Alexander (1920) notes that the papillae are frequently used as an aid to locomotion. Presumably they are osmoregulatory organs as in *Aedes* (Wigglesworth, 1933).

As already mentioned (p. 281), the presence of statocysts seems to be associated with swift movement through the mud. They are present in the predatory *Limnophila* but absent in *Pseudolimnophila*, *Oxydiscus* and *Epiphragma*. They have also been observed in all the Eriopterini encountered except *Gonomyia*. They are lateral sacs on the stem of the somewhat elongated terminal segment and the opening is screened by a sieve-like grating of bristles. A sensory seta is present in the wall of the sac and the expansion is controlled by muscles. They contain clusters of bodies, sometimes grains of sand, sometimes balls of a chitinous nature, and sometimes both. They were first mentioned by Grobben (1876) and later described by Graber (1879) while a full description in several genera is given by Wolff (1922). This author thought that they sampled the mud and assessed its water content but Studnitz (1932) after experiments with *Limnophila fuscipennis* concluded that they are statocysts and control the geotactic reaction.

The specialised area around the spiracles is known as the spiracular disc. It is sometimes a flat truncated area (many Limoniini) but is usually surrounded by lobes varying in number from two to eight. A symmetrical star-shaped condition with five or six lobes is probably primitive as it is encountered in all the major groups except Pediciini. These lobes are : dorsal, one in Limoniinae, two in Tipulinae ; two lateral and level with the spiracles ; two ventral, and these last are the most persistent pair in cases of reduction. The disc surface is nude and shining and coated by a secretion of the perispiracular glands (Keilin, 1913, 1944). The lobes are fringed with a row of sturdy bristles, sometimes restricted to the tips, and they usually bear dark plates that give attachment to muscles that can effect an infolding of the disc. There is a tendency for the plates to divide down the middle line so that the lobes can close in a book-like manner. This feature is particularly well developed in Eriopterini and there is some compensation between this infolding and the extent of the hair fringe round the lobes. For when the division of the plates is pronounced the fringes are restricted to the tips (fig. 2), but when it is slight the hair fringes are complete (fig. 1). Thus a hydrofuge cup can be formed either by the contact of the adjacent hair fringes, the primitive condition, or by the apposition of the naked lobe edges and extended by the terminal fringes. In Hexatomini a funnel effect is usually gained by the apposition of hair fringes, often of great length (fig. 7, 8). In Pediciini the dorsal lobe is lost, the lateral lobes reduced, and the ventral lobes lengthened, but without fringes, and in these cases the spiracles lie on the inner faces of the lateral lobes which can be closed. In many Tipulinae the condition is much as in those Eriopterini with extensive hair fringes except that there are two dorsal lobes instead of one (Alexander, 1920), but in the species of *Tipula* encountered in this work the hair fringes are very slight and plate development small. Closure of the disc is then not petaloid but is effected by a crumpling transverse line just below the spiracles. In most of the Limoniini the lobes are reduced or absent so that the very large spiracles lie permanently exposed, but many of this tribe are tube dwellers and no doubt the tubes are always air filled.

(*a*) Eriopterini.

These larvae are all swiftly burrowing forms and as they move through soft mud the burrows behind them do not fill with water and are evidently lined with hydrofuge secretion. They are all gross-feeding forms and the guts are usually filled by a dark column of decayed plant remains, amorphous debris and grit. The numbers of individuals taken when given in this and following sections are of value only as a record of frequency in 11,500 insects obtained by flotation.

Rhypholophus haemorrhoidalis.—Described by Beling (1886) who gives the habitat as wet leaf mould in woods. It was abundant in flotation, about 240 being taken, occurring in every month except August–September, and it was frequently bred. It is distinctive as the only larva taken that is almost black in colour. In the disc (fig. 1) the lobes are about equal, long and with rounded tips, fringed with hair longer than the lobe width and extending to the base of the lobes. All 5 plates are well developed, black, with the pigment laid down in close reticulation and with the feeblest indication of median division; no plates internal to the spiracles. A very stout sensory seta is near the tip of the ventral lobes.

Tl. 29, uncommon, only 26 being taken, mostly in July. The colour is pale brown and it is closely similar to the last in all observed features except that in the disc the plates are pale, not reticulated, and a broad paler band runs down the middle of each lobe. It is probably a species of *Rhypholophus.*

Platytoma cinerascens.—Brown larva, not common in flotation but the fly often emerged in bulk breeding. The disc is closely similar to the last two but differs in that the almost continuous hair fringe is only about half the width of the lobes. The plates are very dark, with confused reticulation, less close than in *R. haemorrhoidalis.* The larva is described by Levy (1919) from among roots and dead leaves in ponds and brooks.

Ilysia maculata.—Described by Beling (1878) from wet earth. Forty-nine were taken in flotation in November but otherwise it was sporadic and generally scanty. It is a pale yellow larva and the lobes of the disc (fig. 3) are prominent but blunt and rounded; fringes restricted near the tips of the lobes, each consisting of about 10 very short setae with the tips split and on each side of the short group about 10 longer normal setae. The plates are dark, with leopard-like spotting, widely and smoothly divided; small plate internal to each spiracle.

Molophilus spp.—Beling (1886) describes *M. ochraceus* and gives the habitat of this and *M. obscurus* as wet earth near running water in woods. Alexander (1920) describes the nearctic *M. hirtipennis*. Keilin (1913) deals with the hydrofuge secretion of *M. bifilatus*. Otherwise the larvae of this large genus with 21 British species seem to be undescribed (Hennig, 1950). Seven species breed abundantly in the mud and 4 of these, *M. griseus*, *M. undulatus*, *M. serpentiger* and *M. curvatus* have been reared from ascertained larvae. Amongst these *M. griseus* is distinctive but the others can be only doubtfully separated by minute characters in the setal fringes and the shape of the dorsal plate of the disc. Therefore in the record of floated larvae the prevalence of *Molophilus spp.* is recorded as a complex, Tl. 14, and includes also *M. ochraceus*, *M. cinereifrons* and *M. appendiculatus* which have emerged freely from the mud in bulk but have not been reared in isolation. They are very prevalent, appearing in nearly every sample, with a total of about 1500. They are pale yellow and readily distinguished amongst our Eriopterine larvae by the ventral head rods ending in hand-shaped plates. This curious recurrence of the hypostome in modified form (p. 283) is recorded elsewhere in Eriopterini only in one species of *Erioptera*, *E. chlorophylla*, by Alexander (1920). The disc (fig. 2) is similar to that of *I. maculata* in general shape and the restricted terminal fringes have the few middle setae very short, flame-like, or tufted. *M. griseus* is distinctive among the 4 ascertained species because the fringes are more prominent and the setae much broadened near the base. All 4 species have the plates of the disc very darkly and uniformly pigmented; dorsal plate undivided and the others divided by an irregular narrow strip; small plates internal to the spiracles. In juvenile larvae the setae at the lobe tips are few in number and of a simple type.

Erioptera lutea.—Described by Beling (1886) and Bangerter (1930) from damp hollows in woods, generally in leaf mould. It is a pale larva, almost white, and it is abundant with about 120 floated. The disc (fig. 4) is as in *Ilysia* and *Molophilus* in shape but the fringes at the lobe tips are of uniformly long setae. The plates are pale brown, widely divided into parallel strips which on the dorsal lobe are joined by a terminal bridge near the tip; small plates present internal to the spiracles. A tiny common larva, Tl. 37, is almost certainly the first instar of this species. Its respiratory segment is siphon-like, cylindrical, with the lobes as minute erect lappets with 2–3 setae at the tips.

Gonomyia lucidula is an undescribed larva but Alexander (1920), Rogers (1926) and Bangerter (1930) describe other species of the genus, recording them from saturated silt and mud. It was scanty and sporadic, only 23 being floated. It is brownish with dense short vestiture rather more spiny than usual in Eriopterini. The lobes of the disc (fig. 5) form 5 low humps on the margin and are completely fringed by uniform very short tufted setae. There is a weak plate on the dorsal lobe; undivided plates involving the spiracles on the lateral lobes, with a dark band joining these 2 plates across the disc; broad narrowly divided plates on the ventral lobes with a prominent sensory seta near the tip.

Tl. 40 is an unidentified larva taken only 4 times and is probably another species of *Gonomyia*. The lobes of the disc are rounded, almost semicircular elevations on the margin; the fringe is of close-set tufted setae, interrupted only at the meeting of the lobes; all 5 plates are divided but bridges at the tips make all of them horse-shoe shaped.

Tl. 42 taken only once is a minute larva, 2 mm. long, and in moult. The antennae and mouthparts suggest affinity with *Gonomyia*. The lateral and ventral lobes of the disc are pointed, fringed with long simple setae; the dorsal lobe is low, rounded, without fringe, but on each side are 3 tree-like sensillae; each lobe has an undivided plate. The spiracles are unlike any others we have encountered or seen described in Tipulidae. They are on short stalks and the opening is a rosette of 6 pores. It is probably a first instar.

No special habits of feeding have been observed in Eriopterini. They seem to feed grossly on rich organic mud and decaying leaf. The spade-like mandibles, generally with blunt fringing teeth, are in keeping with such a habit. In *Gonomyia lucidula* the teeth are exceptionally sharp for this tribe and some special purpose is suggested by this feature but none of those taken retained anything but a little grit.

(*b*) Hexatomini.

In this tribe three distinct forms of spiracular disc occur. The first is of the generalised type, little different from those described in Eriopterini, and it is found with the massive head capsule in *Epiphragma* and with the dissected capsule in *Pilaria nemoralis* and some other *Limnophila* (*s. lat.*). The second type has no dorsal lobe and the lateral and ventral lobes are long, finger-like, trailing, and without fringes. This is known only in *Elaeophila* (fig. 6) and in company with a dissected head capsule. In the third type there is also no dorsal lobe and the others are long, flattened, triangular and trailing, provided with fringes of hairs several times the length of the lobes themselves. This type occurs in *Pseudolimnophila* and *Oxydiscus* which have massive heads, and in *Phylidorea*, *Pilaria* (*s. str.*) and other genera with dissected heads. It has been pointed out above (p. 279) that the type of head is not in keeping with the apparent affinities of the imagines and it is now observed that the respiratory mechanism is not in keeping either with this grouping or with head structure. Thus there is a complex problem in the phylogeny of the Hexatomini which is not solved by suggesting that the tribe is heterogeneous. The larvae encountered in the tribe are as follows.

Epiphragma sp.—Three larvae about 10 mm. in length are tentatively referred to this genus after the description of Alexander (1920) and comparison with a specimen of *E. ocellaris* from Dr. H. E. Hinton. The larvae are wood-feeding and have a superficial resemblance to certain timber-feeding Coleoptera, especially Buprestidae, for the head is black, massive and quadrate, the thorax expanded, and the abdomen relatively slender. The mouthparts agree with the description of Alexander except that there is a dentate plate associated with the hypopharynx, not mentioned by him. The spiracular disc (fig. 9) has the dorsal lobe low and the other lobes subequal, about twice as long as wide, and fringed with hair about equal to the width of the lobes. There are no distinct plates but the lobe faces are distinctly darkened and there is the usual strong seta near the tips of the ventral lobes. The general vestiture is short dark fur with outstanding setae on all segments and red creeping welts on the abdomen. The anal papillae are long, tapering, and segmented as in some Pediciini and there are no static organs.

Pilaria nemoralis has appeared about 30 times in flotation and its identification is due to Dr. Hinton. The fly has emerged from bulk mud but was not reared in isolation. It has the predatory type of head as in *Phylidorea* and *Elaeophila* but the disc (fig. 10) is much like that of the last described species with the difference that the dorsal lobe is slightly more pronounced, the blackening on the 4 long lobes is stronger, forming definite margins, and the hair fringe is about half the width of the lobes. Vestiture is short golden fur with conspicuous patches over the static organs and there are 2 ventral creeping welts on the 7th and 8th abdominal segments. It is a strong burrower and very voracious (fig. 18). This larva was described by Beling (1886) and in head and disc it resembles closely *L.* (*Dicranophragma*) *fuscovaria* O.S. and *Limnophila* (*s. str.*) *punctata* Schrank (Alexander, 1920). Bearing in mind the highly modified larva of *L. Pilaria* (*s. str.*) it is clear that larval affinities in *Limnophila* (*s. lat.*) are far from being in accordance with subgeneric arrangement of the adults (Coe *et al.*, 1950).

Elaeophila submarmorata described by Bangerter (1928) who took it on the banks of shady streams. It is abundant and occurred in every month except July with a total of about 220. Vestiture is very pale yellow fur with creeping welts only slightly marked by more spiny hair. The hair on the long finger-like lobes of the disc (fig. 6) is more shaggy than on the body and a few black setae protrude through it. The 4 lobes in burrowing form a fusiform cone holding an air bubble and at a water surface they spread out flatly, bringing the spiracles to the air.

Phylidorea fulvonervosa.—Several species of this genus have been described by Beling (1878), de Meijere (1916), Levy (1919) and Alexander (1920) from such sites as the banks of ditches among decaying leaves. It was prevalent and was taken in every month to a total of 230. Vestiture is short golden fur with slight welts on each abdominal segment. In the spiracular disc (fig. 8) there is no dorsal lobe and the 4 lobes are about twice as long as wide with the lateral pair 0·75 the length of the ventral pair. All are rounded at the tip and fringed completely by hair, short near the base, but elongating towards the tip till the terminal hairs are several times the length of the lobes. In cross-section each lobe is like the quadrant of a circle, the outer curved face and one of the flat sides membranous and the other flat sides made rigid by a plate continuous the length of the lobe. In progression through mud or water the lobes are closed, with the 4 plates making a hollow core to the cone thus formed, while the hairs trail in a twisted cone holding an air supply. The burrow has considerable stability owing to hydrofuge secretion and when the larva comes to rest, often far down in the burrow, the long hairs ray out neatly in the wall. These details are evident in waterlogged cotton wool in a vial. When the larva is in water it usually remains quite submerged but sometimes it is caught by the surface film and the long hairs then ray out and, as Alexander (1920) observed, the tension is such that it employs its head to stroke the hairs free.

Pilaria (*s. str.*).—The larvae of several species have been described (Hennig, 1950) and Alexander (1920) notes their occurrence in mud and soft earth and between decaying leaves in swamps. They have been rather scarce in flotation, only about 50 being taken, mostly 1st and 2nd instar larvae in September–October, 1951. They were not reared in isolation, but *P. discicollis* has emerged in bulk cultures and the larva is almost certainly of this species. They are slender, very active forms, clothed in dark brown fur and without distinct ambulatory areas. In the disc there is no dorsal lobe and the lateral lobes are 0·25 the length of the ventral pair but otherwise similar, narrow and sharply pointed, and the hair fringes are like those of *Phylidorea.* Each lobe has a plate with the black pigment in transverse streaks and the plates narrow towards the tip to a mere streak in the middle of the membranous face. The rigidity of the lobes is partly maintained, however, by the close set sockets of the hairs along the margins. As in all the predatory *Limnophila* (*s. lat.*) the static organs are conspicuous and in this case hold a large number of self-secreted balls.

Pseudolimnophila lucorum has not been abundant in flotation but was taken in each month from March to June and September–December to a total of 50 and was easily reared on decayed leaves. The European species seem to be undescribed (Hennig, 1950) but Alexander (1920) describes 2 nearctic species with which this is in substantial agreement with the curious exception that the antenna is said to have 2 papillae while our larva has only one papilla, as usual, and 2 long setae. The nearctic forms are characteristic swamp insects feeding on plant remains, diatoms and small algae (Hart, 1898, quoted by Alexander, 1920). The larva has, as mentioned above, a highly retractile body and is clothed in long shaggy dark fur through which protrude many outstanding sensory setae, especially on the terminal segment. The anal papillae are very long, finger-like, with cuticle dusky and closely wrinkled, with grit adherent and seemingly not at all retractile. Smooth transparent cuticle is usual on these organs but some *Tipula spp.* show this dirty wrinkled type. The disc (fig. 7) has the lobes sharply pointed, the lateral pair 0·3 the length of the ventral pair, the face of each almost covered by a plate with the black pigment in transverse streaks. The long hair fringes are as in the preceding forms but the black setae, outstanding from the trailing fringe, are an unusual feature, for in other larvae of this type the sensory setae are in line with the fringes. No static organs have been detected. Though it is not an observed fact, we believe that the special features of this larva, like *Oxydiscus* following, are associated with a surface habit in the mud.

Oxydiscus senilis (fig. 17) is one of the smallest Tipulid larvae, measuring only about 6 mm. in length. It has been abundant in flotation, occurring in every month except July with a total of 220. Its body is retractile with pale yellow hair. It was reared in isolation, resting mainly amongst decayed leaves at the surface of the culture. There seems to be no record of laboratory rearing in the genus but the larvae and pupae of nearctic species have been described on supposition (Alexander, 1920) as those of *Adelphomyia* (= *Oxydiscus*) and *O. senilis* conforms to these. The fly has not had a settled place in classification. Alexander places it in Pediciini but Pierre (1924) puts it in a special tribe, Crypterini, with *Crypteria.* Coe *et al.* (1950) have *Crypteria* in Eriopterini and *Oxydiscus* in Hexatomini. Judging by larval features this is the correct place for *Oxydiscus* as it is very close to *Pseudolimnophila* and without it Pediciine larvae form a homogeneous tribe. The 4 lobes of the disc are much like those of *Phylidorea* (above), rather broad, rounded at the tips, the lateral pair 0·75 the length of the ventral pair, and the inner faces angled. One half of each angled face is almost completely blackened and the other is membrane except for a rigid strip running just below the bases of the hair fringe on that side. There are no static organs.

Oxydiscus sp., Tl. 4, is a larva taken only once and was distinguished from *O. senilis* by the shape of the massive head capsule which in the latter is rounded at the side and has the breadth 0·75 the length but in Tl. 4 the head is parallel sided and the ratio is 0·57.

The first instar larvae of *Phylidorea* and *Pilaria* (*s. str.*) differ materially from the later instars in the respiratory structures but they are readily recognised by their characteristic heads and by features developing in ecdysis. Fourteen of the former were taken in flotation, 1 in March and the others in July–October; 13 of the latter were similarly obtained in September–October.

Phylidorea has the terminal segment (fig. 11) slightly constricted at the static organs and behind these it expands into a blunt heart-shaped lobe terminating in 2 minute hairy lobes from which arise 2 very long black setae. The simple pores of the spiracles lie at the bases of these lobes. Two similar long setae arise from the ventral side a short distance before the spiracles and a much shorter, but also prominent, pair are sited dorsally about midway along the segment. The vestiture of the dorsal and ventral faces is fur, like that of the general body, but along the sides run irregular bands of short tufted setae, about 4 deep in the row. The 4 blunt anal papillae are conspicuous. The mounted larvae are from 1·5–3·5 mm. in length.

In *Pilaria* (*s. str.*) the terminal segment (fig. 12) is not constricted at the static organs but is an elongated heart shape and at the tip narrows into a cylindrical siphon. The siphon is about $\frac{1}{5}$ the length of the segment, corrugated and beset with very short spaced-out hairs, and ends in a slight swelling with a crown of short hairs. The simple pores of the spiracles are dorsal and subterminal. Evidently the siphon is to some extent retractile. Two very long black setae, 3 times the length of the segment, are sited laterally near the siphon base and a similar pair arises on the dorsal surface a little way in front of these. Laterally and half-way along the segment lies a cluster of sensillae, viz., a prominent tufted seta, a long simple seta, and a short peg. The vestiture above and below is simple fur as on the body but along each side runs a band of spaced-out short tufted setae. The bluntly pointed anal papillae are conspicuous. The mounted larvae are from 1·5 to 4·0 mm. in length, the longer individuals being near the moult.

When these first instar larvae are approaching the moult the hairs that are to form the long fringes of the next instar appear as a compact ring inside the terminal segment (fig. 12). From the ring, in which individual hairs can be barely detected, the hair endings flange out laterally, behind for the ventral lobes, and in front for the lateral lobes. The same mechanism of fringe development in preparation for the moult occurs also in the later instars. We have also seen it in late instars of *Orydiscus* and *Pseudolimnophila* and it is probably general in all the Tipulid larvae with long-fringed lobes.

Pseudolimnophila lucorum has the stomach loaded with a continuous column of amorphous debris and is evidently a gross feeder in decaying material. *Epiphragma sp.* (?) has the stomach similarly filled with fragments of decayed wood. *Oxydiscus senilis* has the mouthparts of a gross-feeding form but the stomach does not contain recognisable plant material. Of 45 larvae examined for food 15 contain the unbroken, or almost unbroken, shells of testate Rhizopoda including *Euglypha*, *Difflugia*, *Cyphoderia* and *Arcella* (fig. 17). These often lie, 2 or 3 together, with no surrounding debris and have evidently been neatly picked up and swallowed whole. Attention was drawn above to the unusually developed sensillae of the antennae and the unusual form of the maxillae (p. 282) and these no doubt indicate some special habit of life which may well be the selection of these organisms, for these protozoa have not been seen in any other larva. One *O. senilis* has the gut filled with fragments of tracheae as though the softer parts of an insect had been eaten out. Another has a much damaged skin of a *Pericoma* larva, thought to be a moulted skin. The others have either empty stomachs or contain only a small collection of grit. The species is therefore believed to be a feeder on animal protein and Rogers (1933) reports an American species of *Adelphomyia* (= *Oxydiscus*) as having a carnivorous habit.

The predatory species of *Limnophila* (*s. lat.*) take in their prey alive and whole, its retention aided by small spines on the pharynx wall. Very large prey is often taken (fig. 18) and several sorts of food occur in the individual. In 82 *Elaeophila submarmorata* the larvae of Tipulids occur 5 times, Ceratopogonids 13 times, Chironomids 7 times, Oligochaetes 40 times and Copepods (fig. 16) (all Harpacticidae which inhabit such sites as wet mosses) 18 times, while 19 had no food. In 65 *Phylidorea fulvonervosa* the analysis of the prey is much the same except that Copepods occur only once. *Pilaria nemoralis* also gives much the same food analysis. *Pilaria* (*s. str.*) *sp.* is more selective in its prey as might be expected from its very specialised mouthparts (p. 282). In 22 individuals Oligochaetes, or masses of their setae, occurred in 11 and the others were empty. Even the minute first instar larvae feed only on worms.

When Oligochaetes form the food there is a good deal of detritus in the predator's stomach and this is the gut content of the worms. It is very gritty and lies in lumps, quite distinct from the continuous column of material in saprophytic forms. The worm setae make the identity of the food certain as they usually lie in clusters and they are often spaced out as in the living worm even when the tissue has been digested.

It is a matter for surprise that though the very sluggish larvae of *Pericoma* form one of the most abundant groups in the mud no single instance of their use as prey by either Tipulidae or Chironomidae has been observed, apart from the qualified case just given for *Oxydiscus*. It may be that they are unpalatable because of the stout plates and setae of the tough cuticle.

(*c*) Pediciini.

The larvae of this tribe as now constituted (Coe *et al.*, 1950) form a homogeneous assemblage. They have closely similar mouthparts and, in particular, the piston-like hypopharynx is not found elsewhere in the family (p. 283). The spiracular disc is also built on a common plan with the dorsal lobe absent, the lateral lobes reduced, and the ventral pair prominent, with cuticle and vestiture little different from that of the general body. The structure of the antennae, however, is not uniform in the tribe. Three species have been taken in flotation and of these *Dicranota bimaculata* and *Pedicia rivosa*, being common conspicuous insects of the brook fauna, are the best known of all the aquatic Tipulids.

Dicranota bimaculata has been studied by Miall (1893), Wesenberg-Lund (1915) and Levy (1919). Miall records it from the mud banks of small streams and Levy amongst sand and roots in a swiftly flowing stream as well as from ditches. About 150 larvae have been floated from the mud, prevalent from January–May and sporadic in July, September and November. It is a slender active form with dark brown fur and 5 pairs of prominent abdominal pseudopods, bearing 2 rows of strong hooks, rather like the prolegs of a caterpillar, a unique feature in the family. The spiracles lie on the inner faces of 2 humpy lateral lobes which can be closed in a book-like manner, while the ventral pair are long, slender, tapering and retractile, with a group of strong black setae at the tip. The antennae are long, slender and tapering, and end in 2 very small papillae.

Pedicia rivosa has been described by Beling (1878), Wesenberg-Lund (1915), Levy (1919), Wardle and Taylor (1926) and Wardle (1926). It has been reported amongst dead leaves and under stones in streams, in woodland ponds (Brauer, 1883) and from moss bordering a mountain stream (Steinmann, 1908). It has been scarce in flotation, occurring in each month from August–November and in March, only 10 individuals in all. The body is highly retractile and the characteristic pale fur is present but so short that the cuticle is semitransparent. There are 4 transverse creeping welts slightly elevated laterally into humps, and weakly spiny. The spiracles can be infolded to close together and Wardle (1926) suggests that they are functionless. There are no distinct lateral lobes and the ventral pair are similar to those of *D. bimaculata*, with the cluster of black setae at the tip, but relatively much shorter. The antennae are stout and cylindrical, terminating in 2 subequal thin-walled papillae nearly equal to the rest of the antenna in length.

The third Pediciine form taken, Tl. 32, agrees with the description of *Tricyphona immaculata* Meigen given by de Meijere (1916) who collected it in humus mixed with fallen leaves near water. It has been taken only 6 times. The vestiture is pale short fur and there are 4 slightly raised creeping welts on the abdomen. In the disc the ventral lobes are prominent, but short and bluntly triangular, terminating with a group of very weak short setae. The lateral lobes are represented by a flat area that extends to half the length of the ventral lobes. This area is margined by a close-set fringe of short setae which extends and meets in front of the spiracles. These are large and face each other. The mouthparts are typical of the tribe but the antennae are sturdy and cylindrical with a strengthening ring near the base and another at half the length and at the tip there is an acorn-shaped papilla with a green glassy look and a second minute papilla by its side.

No special features have been observed in juvenile larvae of the above forms.

The larvae are all predatory and seize their prey in any position, chavel it, and drag it down without the specialised mechanisms of the predatory Hexatomini. *D. bimaculata* seems to feed chiefly on Oligochaetes but insect remains have been seen in them. Oligochaete setae also appeared in *P. rivosa* but its food had been chiefly insect, one showing 19 Chironomid heads and others Ceratopogonids in abundance. They are very rapacious. In *Tricyphona* Oligochaetes and mites have been seen but no insects occurred.

(*d*) Limoniini.

The larvae of this tribe live in widely varied habitats, being recorded from fungi, decayed wood, below bark, in humous earth below leaves, in mosses and aquatic vegetation from stagnant and swift water. Many live in self-secreted tubes in which they move to and fro, and in keeping with this habit the cuticle is nude and transparent apart from the spinous creeping welts. These are strongly developed both dorsally and ventrally on the abdominal segments and more weakly on the mesothorax and metathorax. The tribe shows the greatest diversity in the respiratory mechanism. Thus, according to Alexander (1920), *Antocha* is apneustic, *Helius* (*Rhamphidia*) has the spiracular disc with 5 nearly equal lobes as in Eriopterini, *Elliptera* has 4 lobes with long fringes recalling the condition in some *Limnophila*, while other conditions are described below. The head structures, however, are uniform in the tribe. They are poorly represented in this mud fauna for flotation revealed only 3 species, 2 of these being very rare. *Limonia nubeculosa* which Beling (Alexander, 1920) records from below leaves in woods has been fairly common and has been reared. About 130 larvae were taken with particular abundance in December, 1951, when they averaged 2 per sample. It is, however, one of the most abundant crane flies in the glade and is probably breeding away from the mud. Often they flew out in small swarms when dusky hollows were inspected. The disc is very distinct from any other form seen. It is abruptly truncated like that of a *Tipula* larva, which this larva resembles in shape and colour, but it is without lobes. The spiracles are widely separated and the oblong field around them is margined by a single row of fine setae, continuous except for a break at the sides where a line of dorsoventral crumpled folding is indicated for closure of the spiracles as in *Tipula*. The 4 corners of the oblong field are rounded and in the upper corners and between the spiracles there is diffuse darkening and in the lower corners a well-defined dark wedge-shaped sclerite.

The other Limoniine forms seen are Tl. 35, taken twice, and Tl. 24 taken once only. Both are sturdy larvae about 11 mm. long and differ in details of the mouthparts which need not be gone over at present. They are alike in the spiracular disc which has a form fitting the description of the large genus *Dicranomyia* as given by Alexander (1920). The terminal segment is flattened below and inclined above with the very large spiracles near the rounded tip. They lie close together on the opposed faces of a depression in such a way that on closure they are facing but on opening they have a dorsal aspect. Behind the spiracles lies a pair of narrow plates representing the ventral lobes and the other lobes are not indicated.

All these forms seem to be feeding on the rich mud and their stomachs contain quantities of diatoms. In *L. nubeculosa* there was no indication of a special juvenile form.

(*e*) Tipulinae.

In this subfamily only species of *Tipula* larvae have been encountered. They are stout, earth-brown very retractile insects with characteristic vestiture of short spiny hair with a tendency to lie in transverse rows. There are no creeping welts but the larvae move quickly over a level surface, though they do not burrow with great speed. The spiracles are large and widely separated and the stigmatic field is nude and shining, surrounded by 6 lobes which are short, rounded and fleshy. They are margined by a fringe of short setae with a distinct break in continuity between lateral and ventral lobes. Internal to these breaks, and below the spiracles, there is always some indication of a pair of narrow transverse plates and it is along this line that a crumpled folding occurs when the disc is closed. At the tip of the ventral lobes there is a clear oval area in which arises the principal sensory seta. The anal papillae are voluminous blunt structures with a dusky folded cuticle to which grit adheres. No static organs have been detected.

The number of British species of *Tipula* is great and many of the larvae are known to bear a close resemblance to one another. A survey of the literature shows that there has been a good deal of confusion in the past. Our own early attempt to separate the floated larvae into species was soon abandoned and they were recorded as a complex, Tl. 25. Three species, *T. maxima* *T. rufina* and *T. fulvipennis* have been reared from the mud and it is likely that there are at least 3 others in the complex as *T. paludosa*, *T. oleracea* and *T. signata* are abundant on trunks above the flats.

Alexander (1920) records the habitat of the species as very varied with some that are nearly, if not quite, aquatic, most living in moist soil near water, others in decaying wood, some in dung and, of course, the crop-destroying species inhabit pastures that are sometimes very dry. When grassland in Leeds parks was cut and stacked in low walls round separate allotments the "leather jackets" remained alive between the turfs after these had become very dry and crumbling.

In the flotations *Tipula spp.* were collected regularly in small numbers all over the flats to a total of 274, but it was noticed that the larger individuals rested especially below stones and in crevices in logs lying on the mud. They were also more abundant below stones at the margin of the brook and on one occasion a close pack of 15 larvae was found in one small crevice, wet but not submerged. In flotation the larvae were collected into a Petri dish of water and of all the Tipulidae taken only the larvae of *Tipula* habitually attempted escape and crept swiftly over the bench. To prevent loss it was necessary to restrain them in closed vessels. It is well known that some species move and feed amongst vegetation through the night.

The gut contents of 60 of the larvae were examined and most contained unselected mud but many contained a high proportion of decaying vegetable matter. Rennie (1917) found that *T. paludosa* larvae lived quite well on soil that contained much humus. Slight carnivorous tendencies occur in some species (Alexander, 1920).

Early instar larvae of *Tipula*, Tl. 23, measuring 2–6 mm. in length were taken from June to December to a total of 75. While similar to later instars in general appearance they show differences in structure. The plate of the hypopharynx has 3 teeth instead of 5 and the hypostome has 5 teeth instead of 7. The antenna is almost sessile while in older larvae it has a long stem. The disc is without distinct lobes and is similar to that from a young larva figured by Hennig (1950). Above the spiracles lie 4 double setae rising from complex sockets (these setae are dendritic in Hennig's figure) and to the sides of these lie a simple seta and another double one. Laterally there is a fringe of 10 long setae with thick bases forming a compact crescent and from this runs inwards to below the spiracles a narrow black bar on the line of folding. In place of the ventral lobes there are ovate plates each with 4 long close-set setae and 4 socketed simple sensory setae. An individual near the moult shows the later form of disc with 6 lobes lying below this early phase.

LARVAE OF CHIRONOMIDAE.

The larvae of the Chironomidae are apneustic and the cuticle is thin, nude with a few exceptions, and shining. They are more typically aquatic than the Tipulidae are, but some species (e.g., of *Smittia*) are found in drier sites and, if it is added that some are strictly marine (Clunioninae), some epizootic, and others can sustain an anaerobic life, the full range of habitats is greater than in the crane-flies. Yet they show no such diversity of structure as do the latter. The head capsule is complete and freely movable on the neck. The mouth-parts are on the same general plan as that of the generalised Tipulid with a toothed hypostome giving rigidity to the ventral region and labium and hypopharynx together in a complex above and behind it (Anthon, 1943). The labium-hypopharynx, however, apart from Tanypodinae, is not provided with any strong sclerites and does not seem to have any particular rôle in the mechanics of obtaining food. In the Tanypodinae there is a strong epilabium, or glossa, far back in the mouth with a narrow stem and a toothed expanded tip which pivots on its base through half a circle and probably pushes on and retains the prey.

The antennae have a large basal joint bearing an annular organ and a flagellum of 3–5 tapering joints. Also arising from the basal joint is a hyaline flat seta often surpassing the flagellum in length. The basal joints of the flagellum often bear special " organs of Lauterborn " particularly complex in *Tanytarsus* (*s. lat.*). A double eyespot is usually conspicuous at the sides of the head. Colour is very varied, white, red, green, violet ; some are banded or mottled with purple ; a few, e.g. *Brillia modesta*, have bold black markings.

The body is cylindrical, or, in a few cases, flattened, and composed of 12 similar segments, the first bearing a pseudopod, bifid and spinous at the tip, while the last segment has a pair of diverging spinous pseudopods. The penultimate segment has dorsally a pair of tufts of setae, " bristle brushes ", usually at the tips of small papillae. It is in this region particularly that sporadic deviations in form are seen and these are apparently induced by the adoption of a drier habitat. Hyaline retractile anal papillae are present in most larvae and often show constrictions as in some Tipulidae. Some larvae of *Chironomus* have similar structures pendulous from the 8th abdominal segment. The first instar larvae resemble the later instars but towards maturity the thorax becomes much swollen so that they can be selected in a condition when early pupation is expected, though some, e.g., *Orthocladius perennis*, have a diapause in the late larva. A pronounced feature of the more abundant species in the mud is the association of individuals of all sizes over long periods of time indicating a prolonged flighting and oviposition (p. 305). Many Chironomid larvae burrowing in mud line their burrows with mucus, thus forming adherent tubes, while others construct portable caddis-like cases.

Chironomid larvae have been much studied and can usually be referred to their genus without difficulty by reference to Goetghebuer (1927), Johannsen

(1937) and Thienemann (1944). In the large genera, however, the difficulty of as yet indeterminate specific characters is met with. In the following account of the forms taken by flotation where a specific name is given the insect has been taken through in isolation and identified by imaginal characters.

(*a*) Tanypodinae.

The larvae are predatory and their usual habitats are in the bottom mud and amongst plants in water (Goetghebuer, 1927). They are at once recognised by the antennae and maxillary palps which are elongated, superficially similar and both retractile ; the mandibles are hook-like ; the epilabium is a strong toothed plate. No forms have been abundant.

Pentaneura binotata, taken in small numbers in every month except July and October to an aggregate of about 70.

P. melanops was taken in small numbers in spring 1951, absent through summer, taken again occasionally from September–March.

Pentaneura (?) *sp.*, Cl. 31, was taken once in November.

Anatopynia notata, one taken in March, 1951, and not again seen till November when 8 were taken, thereafter rare till March.

Tanypod larvae were kept in tubes on water-logged cotton wool and fed on Oligochaetes and the commoner species of Chironomid larvae that occurred in flotation. They are very voracious and often seized food as soon as it was presented. One end of the prey is grabbed by the mandibles and pushed into the mouth. The mandibles push it along with a succession of thrusts and to the naked eye the prey seems to be sucked in, for the process of engulfment occupies less than half a minute. Prey nearly as large as the predator was sometimes taken and they seem to require a lot of food as that given was nearly always consumed by the second day. Preparations of fresh larvae showed that their food naturally consists of Oligochaetes, Ceratopogonid and Chironomid larvae, Copepods and their eggs.

(*b*) Orthocladiinae.

Thienemann (1944) and Hennig (1950) include Diamesinae in this subfamily and they have no distinctive character *inter se*. The larvae are recognised by the absence of those strong characteristics possessed by the other subfamilies.

Brillia modesta, recorded from running water, headwaters of streams and stagnant pools (Goetghebuer, 1932) was one of the most abundant species, about 600 being taken. In 1951 there was an evident peak of abundance (10 per sample) in February, with high numbers through March and April when pupae first appeared. Numbers at once declined and kept low but fairly constant till January, 1952, when they averaged 2 per sample ; pupae appeared in February, probably an earlier response to a milder season.

Brillia sp., Cl. 4*a*, agrees with the description of *B. longifurca* (Thienemann, 1944) and this fly is taken over the flat. It was present in small numbers only in spring 1951.

Paraphaenocladius impensus, found in mossy bogs and stream sources, aquatic and terrestrial (Thienemann, 1944), was abundant, about 500 being taken. It was absent only from June to October. This larva deviates somewhat from the Chironomid form towards a condition found in some terrestrial species of *Spaniotoma* (*s. lat.*). The terminal segment is at a right angle to the subterminal segment into which it can be withdrawn, and the usual bristle brushes are reduced in number of setae. Thienemann (1944) mentions 3 setae in this position and one of our reared larvae has this number; one shows 2 setae; but most of our larvae showed unmistakably one only.

Parametriocnemus stylatus, case-dwelling in moss and running water, seldom in stagnant water (Thienemann, 1944), was taken in small and fairly regular numbers in every month except October to a total of 250.

Metriocnemus hygropetricus (*M. longitarsus* Goet. in the sewage filter literature) is a well-known member of the hygropetric association, occurring especially in springs (Thienemann, 1944) and Lloyd (1944) has recorded it from mud. It is one of the dominant sewage filter larvae. In the present work it occurred regularly in small numbers with a gap from June–December to a total of 90. It is coloured for an exposed life, being purple ringed in early instars and purple mottled when near maturity. It is not tolerant of submergence and, like larvae of *Tipula spp.*, constantly attempted escape from the water dish after flotation. Lloyd and Turner (1936) studied its positive responses to gravity and light. In the filters this habit brings it into the topmost layers, most favourable for food, but unfavourable in periods of filter resting in dry weather. At the sewage works therefore its abundance is much influenced by the character of the summer (Lloyd, 1943). Its dominance in the filters is in part due to the habit of eating its competitors though it is mainly a grazing form. This habit is followed also in the mud, for insect remains are often seen in the stomach.

M. hirticollis is recorded from springs and brooks (Thienemann, 1944), from sewage filters and from mud (Lloyd, 1944). In contrast to the last species it is a white larva, coloured for a concealed life. It was taken in small numbers only in March, 1951, and the fly has not been seen in the present work but in previous years it bred freely from mud in bulk from both the Roundhay and the Gledhow flats.

Prodiamesa olivacea, recorded by Thienemann (1944) as mud-dwelling, was frequently floated from January–April, then absent till August and present again till March, with its greatest abundance in mid-winter, with a total of 220. It has paralabial plates with strong fringes of setae and this striking feature, not present in other genera of Diamesinae, is also a feature of the *Trichocladius spp.* (Orthocladiinae restricted) following.

Trichocladius foveatus is an undescribed larva (Hennig, 1950). It was a common form, floated 250 times, present in most months except June–July, with its greatest abundance in spring.

T. dispar (?) was doubtfully so named by Mr. Freeman. It was infrequent and sporadic in flotation with a maximum of 6 larvae in March, 1952. It was distinguished from *T. foveatus* by distinct antennal differences.

Limnophyes complex. Thienemann (1944) gives the habitat for the genus as marginal as well as terrestrial. These were among the tiniest larvae and many of the younger forms did not rise from the sedimented mud so that the aggregate of 400 recorded is certainly an underestimate. They were taken in each month except August and included *L. prolongatus*, *L. pusillus* and an undescribed species distinct from *L. pusillus* by the possession of scales on the thorax and an anal point in the male. In bulk breeding 765 *Limnophyes* emerged in the proportions of 39 per cent., 50 per cent. and 11 per cent. in order of the species given. *L. minimus*, one of the most abundant filter flies, was taken over the mud but not reared in the present work but Lloyd has bred it from this site. *L. pusillus* is an occasional filter fly and is parthenogenetic in the filters, though in its natural haunts the sexes are equal.

Orthocladius piger was one of the most abundant forms in flotation, about 400 being taken. It was almost confined to the winter months and outside these a small number was taken in August–September only. In 1951 the pupae were floated in March and the fly was taken free in April. In 1952, after the milder winter, pupae were seen in January and the fly was taken in February.

Orthocladius sp., Cl. 26, has interest as it was the only Chironomid species, apart from the rare forms, floated only in the warmer months. It appeared in fairly regular small numbers from May to September to a total of 74 larvae.

Corynoneura scutellata was reared from a small number of larvae floated from August–November 1951. The genus includes the tiniest of the British Chironomids. *C. scutellata* and an unidentified *Corynoneura* were taken over the flat in November only and then abundantly. They were dancing among holly bushes in weak sunlight in small swarms when no other flies were seen active in the glade.

Nine other species of Orthocladiine larvae were floated once only, or in very small numbers, and not reared. Cl. 19*a* and Cl. 28 by antennal structure seem to be near *Metriocnemus* (*s. str.*) ; Cl. 16 is a form with outstanding long setae along the body ; Cl. 33 has a characteristic hypostome, elongated with the surface in many longitudinal ridges ; Cl. 22 is quite exceptional in the hypostome which is an elongated sharp triangle with no side teeth and the 2 larvae taken have been feeding on decayed wood. These 5 species have the typical Chironomid form but in the remaining 4 species the bristle brushes are lost, or modified, and the anal segment variously adapted. They are all identical with, or very near, forms figured by Thienemann (1944) and described as terrestrial or amphibious. They are :

Cl. 3 near *Pseudorthocladius ;* bristle brushes as single setae $\frac{1}{3}$ the length of the body; posterior pseudopods slender with 4 claws only. Taken 13 times.

Cl. 15 near *Pseudosmittia trilobata ;* no bristle brushes ; posterior pseudopods reduced, with 2 claws ; anterior pseudopods short, dome-like ; antenna characteristic, with enlarged curved seta. Taken once.

C. 10 near *Euphaenocladius* (*Phaenocladius*) *aquatilis ;* anal margin ringed with teeth and retractile, as in *Dasyhelia ;* no bristle brushes. Taken twice.

Cl. 15 near *Bryophaenocladius* (*Orthocladius*, Group B, Edwards) ; preanal segment is swollen and the anal segment, bent ventrally, is retractile into it ; posterior pseudopods with a dome of short claws ; no bristle brushes. Taken twice. This modification recalls the larva of *P. impensus* which is also amphibious.

(*c*) Chironominae.

These larvae are distinguished by the possession of paralabial plates with fan-like striations at the sides of the hypostome. Within the subfamily *Tanytarsus* (*s. lat.*) larvae are distinct because the antennae arise out of definite sockets and there are pairs of feathered hairs on the sides of the body segments.

Chironomus (*s. lat.*) was poorly represented in the flotations for in the whole series only 11 were taken and these included 3 species, none of which was identified. *C. albicornis* and *Microtendipes nitidus* were bred in small numbers from mud in bulk. *Tanytarsus* (*s. lat.*) was better represented.

Microspectra subviridis was by far the most abundant larva of any type taken, about 1600 in all being collected. It occurred in every month except September, but in 1951 it was ten times as abundant as in the following year. In the early months of 1951 the whole sample of mud in a few cases was riddled and spongy from their long mucus tubes with their adherent grit and in one sample in January some hundreds (200 removed) were present, while the average for the month was 1 in 4 ml. of mud.

Stempellina bausei is a well known larva (Goetghebuer 1928). It lives in caddis-like cases of grit and, unlike *M. subviridis*, it does not leave the case in flotation so that the few that were taken were from the sedimented mud. Many may have been overlooked as the case is only 4 mm. long and very slender.

Larvae of Psychodidae.

The Psychodidae are divided into 4 subfamilies of which Psychodinae with the 3 genera *Psychoda*, *Pericoma* and *Telmatoscopus* form an element of the mud-flat fauna. There is general uniformity in the larvae of these in that the 3 thoracic and the 1st abdominal segments are constricted into 2 subsegments and the 2nd to 7th abdominal into 3 subsegments. They are amphipneustic and the anterior spiracles lie at the tips of low pegs while the posterior pair are at the tip of a rigid conical siphon which ends in a fringe of hydrofuge hairs on 4 lobes. The head is strong and eucephalous and the whole ventral surface is flattened for creeping.

In *Pericoma* and *Telmatoscopus* each subsegment bears a dorsal plate, 26 in all, usually with upstanding setae. In *Psychoda*, though some have the full complement of plates, there is a tendency for reduction from before backwards, till in extreme cases only the 2 posterior plates are present (Satchell, 1947). In all 3 genera the cuticle is very tough and in it are inserted denticles, useful in identification. In *Pericoma* and *Telmatoscopus* these are so close set that the larvae have usually a dark or almost black colour, but in *Psychoda* their development is slighter and the larvae pale.

Pericoma larvae and pupae have been abundant throughout the work, 1847 being taken from November 1950, to April, 1952, an average of about one to each 25 ml. of mud floated out. The incidence of the various species is not given because of some confusion in identification. The most complete work on the genus is by Satchell (1949), but although descriptions are given for 15 of the 24 British species, the others are not known. Of those described by Satchell the following were bred through and checked against his descriptions: *P. fusca*, *P. fuliginosa*, *P. trivialis*, *P. canescens*, *P. neglecta*, *P. blandula* and *P. pulchra*. Five species whose larvae are not described emerged from the mud in bulk and of these *P. pilularia* and *P.. crispi* were abundant, scarcer forms being *P. gracilis*, *P. palustris* and *P. avicularia*. The larvae of *P. crispi* were defined late in the work but some at least of the others must have been passed unrecognised.

The larvae are very time absorbing and, with their black features on a black background, exhausting to the eyes. The group of larvae with 10 or more setae on the sides of the siphon give most difficulty. They move exposed on the mud surface carrying a masking load of adherent mud, only to be dislodged by vigorous shaking. Of these, *P canescens* is distinct amongst the known species because the setae are raised on prominent bosses. In *P. trivialis* the locomotory lobes along the sides of the body bear a cluster of feathered spines (Satchell, 1949) while in *P. crispi*, otherwise a similar larva, these spines are stout blunt denticles.

There is a further possible confusion between *Pericoma* and *Telmatoscopus*, for Satchell (1949) observes that the larvae of very few species of the latter are known and quotes Feuerborn for the statement that *P. trivialis* and *T. ustulatus* are much alike. Two species only of *Telmatoscopus* have been bred from bulk mud and taken free in this work, *T. tristis* and *T. soleatus*, and the latter has been reared once from a floated larva. This larva of *T. soleatus* would not be confused with any known *Pericoma* for the dorsal plates of the sub-segments are tiny oval sclerites with evanescent setae. The larva of *T. tristis*, however, remains unknown and as it was at times an abundant fly, its larva may have been taken and passed as a *Pericoma*.

No larvae of *Psychoda* have appeared in the flotations but *P. severini*, *P. cinerea* and *P. setigera* were floated out as pupae in small numbers. These and *P. gemina* emerged from the bulk mud while *P. alternata* was taken above the flat in a recently emerged condition and apparently breeds there. This last species, so characteristic of sewage filters, was bred abundantly by Lloyd from Gledhow Valley mud but not from the present site. The other filter species of *Psychoda* are *P. severini* and *P. cinerea ; P. gemina* is recorded only from mud and ditch bottoms ; *P. setigera* has hitherto been recorded only from field cow dung. *P. grisescens*, also a field-dung form, was bred by Lloyd from Gledhow Valley mud. *P. albipennis*, recorded from dung and a wide range of decaying plant materials, has not appeared in the mud though it breeds freely in a leaf tip above the Roundhay mud. The other British *Psychoda* with known larval habits are all field-dung forms (Satchell, 1947*a*). All the species of the genus are shallow burrowing forms keeping the siphon tip at the surface except *P. brevicornis* which is a flattened surface species with a reduced siphon and buoyant branching setae. They are saprophagous insects though the species that haunt the filters are there feeding on the algae, fungi and bacterial and protozoal film.

By contrast, the known larvae of the British *Pericoma* are nearly all creeping surface forms and their long stiff setae would interfere with burrowing. The exceptions mentioned by Satchell (1949) are *P. fusca*, with reduced setae and an elongated siphon, which has the *Psychoda* habit, and *P. fuliginosa*, also with reduced setae, which lives in cracks and crevices and below sticks rather than on the surface. *P. pulchra* with a very flattened form and branching buoyant setae is the analogue of *Ps. brevicornis* in that by similar devices it is almost unsinkable, but Satchell, who took it under stones and leaves close to springs and clear flowing streams where it could be kept wet by lapping, thought that the adaptation was for closer contact with the substrate on the analogy with many aquatic forms in swift water. It is, however, one of the commoner larvae of the mud. All the environments mentioned by Satchell for *Pericoma* are of marginal nature though special in some cases, e.g., *P. trifasciata* and *P. calcilega*, neither taken in this work, are from limey springs and streams, while *P. neglecta* is from clumps of moss on waterfalls and only 2 of its characteristic larvae have been taken in our flotations. Satchell (unpub.) found *P. trivialis* breeding in the sewage filters at Windermere. The larvae of *Pericoma* are phytophagous or saprophagous and in particular they feed on the softer tissue of decaying leaves which they skeletonize and this was the material usually given in isolated breeding. Pupae were abundantly taken in flotation and when placed in vials proved extremely restless and unusually subject to moulds.

Some idea of the relative abundance of *Pericoma* species in the mud is given by the data of flies emerging in bulk breeding. One *P. palustris* and 3 *P. avicularia* appeared but no *P. neglecta*. Of the 878 others recorded the proportions were : *P. trivialis* 37.3 per cent., *P. fusca* 25·6 per cent., *P. fuliginosa* 12·5 per cent., *P. crispi* 8·2 per cent., *P. canescens* 5·2 per cent., *P. pulchra* 4·6 per cent., *P. pilularia* 3·5 per cent. and *P. blandula* 2·8 per cent. Freeman (1953) recognised *P. crispi* as a then undescribed species but stated that amongst the material submitted there was a small proportion of *P. gracilis*.

LARVAE OF CERATOPOGONIDAE.

The larvae of Ceratopogonidae are apneustic, with a eucephalous head and 12 body segments. Anterior pseudopods are present only in the *Forcipomyia* group, while the posterior pseudopods are represented only in the *Dasyhelea* group where they take the form of a hook-bearing lobe eversible from the anus. In the former group, which includes mainly terrestrial forms, the cuticle is beset with setigerous lobes but in the others it is extremely smooth and shining, a condition that aids the movement which is snake-like with lateral waves. So swift is this in the younger larvae especially that they seem to flicker through water or thin mud. The head is elongated and pear-shaped. The antennae are usually one jointed and the eyes usually composed of 2 ocular spots placed close together. The hook-shaped mandibles are generally without teeth and work vertically and seem adapted rather to scrape in the food than to fragment it (Kieffer, 1925). Maxillae are reduced but the hypopharyngeal apparatus is highly elaborate, set far back in the mouth and furnished with combs of teeth.

These larvae form an important part of the mud fauna and many appeared in the flotations. They were collected to the number of 790 but many of the younger larvae of *Culicoides* would be missed as they remained often in the sediment. A number of species were bred but the larvae were not sorted except into groups. They comprised 240 of the *Palpomyia-Stilobezzia* group, distinguished by the group of strong black setae on the terminal segment while the rest were *Culicoides* with a very few *Dasyhelea sp. Forcypomyia*, which, with species of *Culicoides*, breeds occasionally in sewage filters, was expected but did not appear. The species present and their relative abundance are judged from the emergence of the flies from mud in bulk. In the *Palpomyia* group, of 300 flies the proportions were *P. flavipes* 43 per cent., *P. quadrispinosa* 22 per cent., *P. serripes* 11 per cent., *P. nemorivaga*, 1 fly, and *Stilobezzia gracilis* 23 per cent. In the *Culicoides* group of 500 flies *C. vexans* gave 96 per cent., *C. pulicaris* 3 per cent., *C. obsoletus* and *C. odibilis* each 1 per cent., and *C. impunctatus* 2 flies. *C. stigma* was reared from the Gledhow mud but not from this site. *Dasyhelea sp.* was rare both as floated larva and bred fly.

LARVAE OF CULICIDAE.

Species of *Anopheles*, *Culex*, *Aedes*, *Theobaldia* and *Chaoborus* were taken on the tree trunks but none emerged from bulk mud or were seen in flotation. *Dixa nubilipennis* was the only member of the family found breeding in the mud. The larvae of *Dixa*, usually associated with the surface film in water, are well known, though this particular species is undescribed. It was abundant in flotation with 400 larvae and pupae, peak periods being in February and October with relatively few at other times. The flies were seen active only in October. They were reared without difficulty on filamentous algae, abundant in the stomachs of floated larvae. Malloch (1917) gives the habitat of the genus as in springs and clear mountain streams and the food as algae while Stempell (1925) records them as marginal forms.

LARVAE OF MYCETOPHILIDAE.

The general habitat of the family is in decaying vegetable matter of many kinds. As the larvae are holopneustic they are clearly not true mud forms, and a few larvae of *Sciara sp.* floated may have been associated with bits of decaying wood. The flies emerged in small numbers from the mud in bulk.

LARVAE OF TRICHOCERIDAE.

Hennig (1950) and Coe *et al.* (1950) give the habitat as decaying vegetable matter and living vegetation. *Trichocera maculipennis* is recorded as swarming in a filter at a distillery (Karandikar, 1931) and species breed occasionally in sewage filters. Three species were abundant over the mud and the larvae were expected in flotation as they are well adapted for a wet life, but only 4 were taken in the whole series and no flies emerged from bulk mud.

LARVAE OF PTYCHOPTERIDAE.

These long-siphoned metapneustic larvae are admirably adapted to a mud life and their habitat is recorded by Hennig (1950) as water, swampy earth and decaying vegetation, while Kratochil (1936) found them in moist earth in woods. Larvae appeared infrequently in flotations in spring 1951 and were thought to be of two species but were not reared. *Ptychoptera albimana* F. was the only species taken as a fly in the glade.

LARVAE OF ANISOPIDAE.

Anisopus larvae feed on dung or the liquid running from manure heaps, fermenting sap, decaying plant roots, etc. (Coe *et al.*, 1950) and in house sinks. *A. fenestralis* Scopoli (for some time confused with *A. cinctus* F.) has long been known from sewage filters locally, but since about 1942 it has invaded many filters in the North of England and has become one of the dominant sewage flies and a serious nuisance in places (Lloyd, 1945). This species as well as

A. punctatus F. and *A. cinctus* were taken on trunks over the mud and are probably breeding there, but not freely as none were seen in flotation, nor did they emerge from bulk mud.

LARVAE OF OTHER DIPTERA.

Larvae of Brachycera and Athericera were scanty in flotation, and as the abundant Nematocera absorbed nearly all the time available, very little can be said about them. They totalled for the whole series less than 200 larvae and pupae of which 45 were classed as Empididae, 65 as Syrphidae and 3 as Stratiomyidae. The tentative groupings of the others, many of which were small and immature, are too uncertain to be worth recording. Tabanidae are not seen in the immediate environs of Leeds. Of the Empididae the majority were *Hemerodromyia praecatoria* Fallén and a closely allied species. *H. praecatoria* is described by Brocher (1909) from the rocky bottoms of brooks and Hinton (1951) recently drew attention to the adaptation of the remarkable pupa, seen several times in this work, to either wet or dry conditions. They are provided with serial cuticular gills of great length and slenderness. Attention may also be drawn to *Tachypeza nubila* Meigen which is one of the commonest insects on the trunks over the mud. It is seen waiting for its prey on nearly every trunk in a season that lasts from spring to early winter. In Dolichopodidae *Campsicnemus curvipes* Fallén and *Argyra leucocephala* Meigen were reared from the mud. The habitat of the former is recorded as aquatic (Malloch, 1917) and the latter as in mud (Marchand, 1918). In Syrphidae, only *Chrysogaster splendens* Meigen and a species of *Cheilosa* were reared. No Stratiomydae emerged during this work but Lloyd has previously bred *Geosargus sp.* from the site. No Borboridae or Ephydridae were bred from the mud in the present series or that of Lloyd, but the latter reared great numbers of 2 species of *Borborus* and a few *Scatella sp.* from the fouler mud of Gledhow Valley. In the former family both *Borborus spp.* and *Limosina spp.* breed in sewage filters but not very successfully. *Scatella stagnalis* Fallén and *S. silacea* Loew also breed in these places and the latter in the last few years has greatly increased at several sewage works near Leeds, notably at Bradford where in some recently constructed filters Terry (1952) records it emerging at rates up to 750 per sq. ft. filter surface per week and their clusters on the concrete pillars at the filter ends were conspicuous from a great distance and looked, till near approach, like patches of tar. Such a density rivals that of any of the habitual sewage filter flies. This experience and that of *A. fenestralis* quoted above show that the sewage filter fauna is not so static as it appeared to be during the 8 years of continuous fly trapping recorded by Lloyd (1943*a*)

COLEOPTERA.

Beetles and their larvae floated up very readily and a remarkable feature of the collection is that in the whole series of samples only 23 adults and 29 larvae were taken. The larvae were composed of 11 Carabidae, 12 Staphylinidae, 3 Dytiscidae and 3 not assigned to the family. The adults were as follows:

Carabidae: *Agonum ruficorne* Goeze.

Hydrophilidae: *Helophorus flavipes* Fabricius, *Hydraena nigrita* Germar, *Limnebius truncatellus* Thunberg.

Silphidae: *Nargus velox* Spence.

Staphylinidae: *Micropeplus tesserula* Curtis. *Lesteva heeri* Fauvel, *L. longelytrata* Goeze, *Olophrum piceum* Gyllenhall, *Omalium rivulare* Paykull, *Atheta sp.*

OTHER INSECTS.

Collembola came to the surface at once when the mud was well stirred in the floating fluid. They were not sorted or counted and though a few were seen in every sample their numbers were not great. The average would have been some 5–10 per sample. Far greater numbers harboured in the carpet of fallen leaves in parts of the glade away from the mud.

Plecoptera were represented by 3 nymphs only and Trichoptera by *Beraea pullata* Curtis, which is evidently a denizen of the mud as it was taken with fair regularity in small numbers. Its bent conical case of sand grains was detected in the sedimented mud by the tracks made and no doubt was often missed. The caddis *Crunoecia irrorata* Curtis also emerged from the mud in bulk. No Ephemeroptera or Odonata were encountered in flotation.

DISCUSSION.

Lloyd (1944) has shown that the grazing fauna of sewage filters is derived from that of the mud flat and it is of interest to compare these environments and to speculate on the fact that only a small quota of the latter association has colonised the filters. Most of the mud breeding forms must from time to time gain access to the filters either through their own volition or through accidental carriage there of their early stages in the sewage stream. Why do so few survive to become permanent and successful members of the filter fauna? Some filters receive a strong chemical sewage which restricts even the habitual fauna to one or two species but in most the sewage is chemically innocuous and if the filter is not being overloaded and its crevices choked the oxygen supply is unbounded. The answer therefore is to be found rather in the physical conditions of filter life and in restrictions on the types of food available.

In the filters the full effects of seasonal change are not felt. Frost rarely penetrates them and the temperature fall at night is little. They are fully exposed to sun and though they do not dry out deeply when the sprinklers are at rest there is considerable mortality of insects and worms in the topmost layer when there is stoppage in hot bright weather. This is important for those forms which prefer a shallow location for feeding or pupation and it could debar many mud breeding species. The general equable conditions aid the multivoltine insects, for these maintain some activity through the winter months when under outside conditions they would be almost or quite at a standstill. Therefore an active population of larvae, pupae and, in some cases, adults, is ready to burst into active breeding at the first substantial rise of temperature in spring and, at the other end of the year, they are able to continue breeding when the same species in nature have gone into winter conditions. In consequence, insects that could achieve only two or three generations in nature can in the filter manage from four to eight generations according to species (Lloyd, 1945). The restless winter conditions may make the filters intolerable for some potential colonisers in which a winter rest is obligatory.

In the mud flats, the mud being shallow, the full effect of winter is felt, for even in the two mild winters experienced during this work the mud was on several occasions frozen solid and overlaid by a layer of ice embedding the blanket of leaves. This freezing, however, had no apparent effects on the insects as samples of the mud had a similar population before, during, and just after the frosts (p. 278). The blanket of leaves present in autumn and winter does not appear to afford much protection against chilling and it is probable that the nocturnal temperature fall follows fairly closely that of the air. The tree cover in the warmer months is such that protection is given from direct sunshine, but in prolonged dry weather the edges of the mud contract and the seepage lines become less wet. It is not known whether this causes mortality in the mud dwelling insects, but probably it does do so.

Samples of the mud brought to the laboratory during the cold months held many larvae but few pupae, for of the latter only a few of the Orthocladiinae pupated in nature before the winter was over. Under warm conditions these samples gave rise to few adult insects so it would appear that most of the mud forms naturally spend the winter as more or less quiescent larvae. Species without this restriction, for they showed winter emergence, included *Limnophyes prolongatus*, *L. sp. incog.*, *Paraphaenocladius impensus*, *Palpomyia flavipes*, *Culicoides vexans*, *Molophilus ochraceus*, *M. undulatus*, *Erioptera lutea*, *Ilysia maculata*, *Pericoma trivialis*, *P. crispi*, *P. fusca*, *P. canescens*, *P. pulchra*, *P. pilularia*. These are for the most part species which were particularly amenable to the artificial conditions of cylinder culture as they were amongst the more abundant species emerging in summer.

Coe *et al.* (1950) record the months in which the imagines of many British Chironomidae have been taken. The records show that prolonged seasons of flight, and consequently of oviposition, occur in many species. This aspect of the behaviour of the species has been reflected in the collections of larvae, for frequently a single collection has yielded recently hatched, half-grown and full-grown larvae. Particular cases in which this has been noted are: *Brillia modesta*, *Prodiamesa olivacea* and *Microspectra subviridis*, the flighting records being respectively 1, 3–10; 4–11; 2–11. Some measurements were made in *B. modesta* in January–February, 1951, and the following record of length was gained : 5 6·5 mm., 1 6·0 mm., 6 5·0 mm., 7 4·5 mm., 6 4·0 mm., 5 3·5 mm., 4 3·0 mm., 2 2·5 mm., 8 2·0 mm., 7 1·5 mm. This is a uniform scatter over the whole possible range of size at a time when progress must have been very slow. The very prolonged flighting period is probably restricted to insects of a saprophytic habit and the like in contrast to the very many whose pattern of seasonal incidence is bound up with the phases of some particular plant food.

The basic food supply in the filters is steady and continuous and builds up into the active film of bacteria, fungi, and protozoa together with a thick covering of the alga *Phormidium* on the surface of many filters. This growth is wholly edible to grazing larvae and in autumn and winter is superabundant, but in spring, with increased grazing, it becomes depleted and its remnants are largely shed in the "vernal slough." Food is then insufficient for the potential population and the Chironomids with a carnivorous capacity tend to thrive at the expense of the sluggish *Psychoda* (Lloyd, 1943, 1945). There are no obligatory predaceous insect larvae in the filters as a rule though spiders are fairly numerous.

In the mud flats the basic food supply is the blanket of leaves that forms in autumn. This is slowly incorporated into the mud through winter and the leaves are softened by decay and skeletonised by grazing larvae and worms, some quickly, like oak and sycamore, and others slowly, like holly leaves. There is no process analogous to the filter sloughing and probably never any shortage of food for the grazing larvae or gross feeding forms, for even if the leaves should be all consumed there still remain the more slowly decaying twigs and bits of wood with their associated organisms, while there is always some shedding from the trees and evergreen shrubs. On the lower flat there is also the early summer decay of a brief rich cover of celandine which clearly adds a good supply of organic matter to the mud.

The basic factor in the nutrition of the saprophytic forms, and through them of the predaceous species, is doubtless related to the volatile quota of the medium in which they live. Tomlinson (1946) estimated the volatile matter in a number of samples of dry filter film and found it to vary from 48–71 per cent. A number of estimates were made of the volatile matter in the dried mud from January to April and the average was found to be 18 per cent with a range of 14–27 per cent. The variation in various parts of the flat was erratic and no seasonal diminution was observed. The densities of population which may be related to the volatile fraction are discussed below (p. 308).

The greater stability of the food supply in the mud flat during the early summer is probably a factor of great importance in the regulation of the fauna. At this time the flighting of the Nematocera over the flat is at its maximum while that over the filters has just passed the peak of the year. Thus in the filters the food supply has then been reduced to its lowest ebb by intensified grazing and remains low till early winter and would-be colonisers from the mud produced species would expose themselves to the most vigorous competition for food. There is no reason to suppose that there is any competition of this type in the mud flat.

Two other factors may be mentioned as of certain importance in restricting greater colonisation of filters from the mud. The first of these is suitability of diet, for though the film is nutritious to some grazers its qualities, such as consistency, may debar others. Those for instance that skeletonise leaves might find the diet too soft or otherwise too different from their normal food. The second factor concerns the attitude and bodily support required and a suitable site for pupation. It is the habit of Tipulid larvae that dwell in mud mainly to burrow and rest with the elaborate respiratory area flush with the surface, or connected to the surface by a channel. This positioning would be impossible for insects of such size in filters of the usual large grades of medium. The pupae of the Hexatomini and Eriopterini have the unusual feature for aquatic Nematocera of open spiracles along the abdomen as well as the thoracic breathing horns and they are very sensitive about their pupation sites. Most aquatic Tipulidae leave the water and pupate in soil (Alexander, 1920). The constant wetting and other disturbances would be harmful to them. Any mucous tubes formed for larval life would most certainly be eaten for it is a significant fact that no tubicolous larvae live in the filters though some, such as *Chironomus riparius*, *C. dorsalis* and *Tanytarsus atrofasciatus*, breed abundantly in the gutters below the filters.

The mud flat differs from the filter in the predaceous elements in the fauna for many obligatory carnivorous insects are present in the former. These are the larvae of the Pediciini, some of the Hexatomini and the Tanypod Chironomids. They are all very active hunting larvae and apparently disperse and travel widely about the mud, for no concentration has ever been observed in any flotation sample though few samples have been without some of them. In this, as expected, there is a difference from the saprophagous species in which concentration is often found. Their abundance may be judged by the fact that they form 6·4 per cent. of the observed larval population. Attention has been drawn to their rapacity and they must exert a substantial reduction in small worms and larvae.

Although much study has been given to the organisms inhabiting fresh water mud, no attempt to assess the density of the populations in this environment seems to have been made. Most of the work of this type has been concerned with the fauna of grass field soils. The most complete of these studies is that of Salt *et al.* (1948) who, by freezing, thawing, graded sieving and flotation with a benzene interface obtained estimates that included all organisms down to a size of 0·2 mm. In an average aggregate of all Arthropods they record just under 1 per ml. of soil while the maximum from the top 6 inches was 3 organisms per ml. Their figures show a relative abundance of selected groups as follows : Diptera 1/300, Coleoptera 1/50, Hemiptera 1/20, Collembola 1/4 and Acarina 1/2. The last two groups were overwhelming in numbers, accounting for about 5/6 of the total population.

At the other extreme the film in sewage filters maintains an enormous population of Diptera and these are dominated, as is well known, by a small number of species. Some Collembola, especially *Achorutes*, are abundant locally and occasionally mites swarm on the medium. The small worm *Lumbricillus lineatus* abounds at nearly every sewage works and is occasionally sufficiently abundant as to impede the flow. Though the distribution of the film to a great depth and its complete edibility make comparison with either a soil or a mud fauna difficult, the following data taken from Lloyd (1944*a*) are of interest in this connection. Samples of surface medium (stone plus film) measuring 1600 ml. were washed clear of film and the bulk of this was measured and the insects and worms counted. Collembola and mites were absent. In a dirty overloaded filter threatening to pond, the film was 280 ml. and included 380 worms, *L. lineatus*, and 17 *Psychoda* larvae and pupae per 1 ml. ; no Chironomids present as conditions were too foul for them. In a filter of average cleanliness and working well the film was 180 ml. and included 53 worms, 10 *Psychoda* larvae and pupae, and 0·2 *Metriocnemus* l. and p. per 1 ml. In a very clean filter, also working well, the film was 50 ml. and included no worms (film insufficient) or *Psychoda* but 30 *Metriocnemus* l. and p. per 1 ml.

The specialised nature of the filter fauna is almost extreme as the following data for trapped emerging insects and spiders shows (Lloyd, 1943, 1945 and part unpublished): Trapping on the Knostrop (Leeds) filters over an average of 2½ sq. ft. through 8 years continuously 520,000 forms were taken, 99·7 per cent. of them belonging to 5 species of filter flies that emerge throughout the year as weather permits, *Metriocnemus hygropetricus*, *M. hirticollis*, *Limnophyes minimus*, *Psychoda alternata* and *P. severini*. *Orthocladius perennis* Meigen, occasionally a dominant sewage fly, but hampered by the summer prepupal diapause, was present to the extent of 0·16 per cent. The remainder, 0·14 per cent. of the total catch, consisted of 1/9 other Diptera, 1/3 Coleoptera, 1/40 parasitic Hymenoptera, 1/100 Collembola and 1/3 spiders. In all the trapping at Knostrop and other filters in the district, 72 species were taken and identified through the Commonwealth Institute of Entomology. These included 10 very prevalent species, 6 mentioned above and 4 others that share with these the faculty of continuous breeding, *Psychoda cinerea*, *Anisopus fenestralis*, and the Collembola *Achorutes subviaticus* Bagnall and *Tomocerus minor* Lubbock. *P. cinerea* and *A. fenestralis* were not breeding in the Knostrop filters at this time, though the latter invaded them about 1942 and has since become one of the dominant species there. Nine other species were common but their seasons of emergence were restricted so their abundance in the grand total is masked by the continuously breeding species. These were Borboridae, *Leptocera limosa* Fallén, Mycetophilidae, *Sciara auripila* Winnertz, Staphylinidae, *Platystethus arenarius* Fonscolombe and *P. alutaceus* Thomson, *Oxytelus tetracarinatns* Block and *O. nitidulus* Gravenhorst, *Atheta elongatula* Gravenhorst and *A. zostovae* Thomson, Hydrophilidae, *Cercyon ustulatus* Preyssler.

Twenty-four species, chiefly Staphylinidae and Borboridae, were rare, being taken only about 2 5 times. Thirty species of small beetles and flies were represented by single captures and were probably mainly stragglers, not bred in the filters. The bed bug, *Cimex lectularius*, was taken twice, seemingly unaffected by its water conveyance.

In the flotations of mud, samples of 125 ml. were used in the first year of work and later samples of 250 ml. were taken and floated in equal parts. Thus in all 342 samples each of about 125 ml. were examined. The sorting and attempted identification of Nematocerous larvae entailed so much work at the microscope that it was not practicable to deal with all the forms that floated, so Collembola and Acarina were ignored. Both groups occurred in most samples but never in great numbers. In particular, Collembola were very scarce in comparison with the swarms seen under the blanket of leaves away from the mud areas. Oligochaetes, chiefly Tubificidae and Enchytraeidae, were counted in the samples taken from November, 1950, to March, 1951. In 62 samples the average number was 29·2 worms per sample with a range of 0–121. The lower limit of size of the forms more closely examined was fixed by what could be seen with a reading glass on the water surface, or in the sedimented mud, and lifted by forceps into the collecting vessels, i.e., about 1·0–1·5 mm. Few of the mounted larvae measure less than 1·5 mm. In all 11,573 insects were taken, giving an average of 34 per sample or 0·27 per 1·0 ml. This is a far lower density than that recorded above for the film of sewage filters and even if the whole cubic space of the filters is considered it is still much lower, for in the table given by Lloyd (1944*a*), where 22 samples each of 1600 ml. medium are recorded, the average density of insects is 0·71 per 1 ml. and of worms 6·4 per 1 ml. This particular series was weighted for worms by readings from exceptionally dirty filters. On the other hand it is far higher than that for organisms of similar dimensions recorded for pasture soil by Salt *et al.* (1948).

Of the 11,573 insects taken by flotation 99·4 per cent. were Diptera. There were only 44 Coleoptera, adults and larvae, 0·4 per cent. of the total, and the remnant included 19 Trichoptera, 3 Plecoptera and 2 Ichneumonidae. Two surprising facts arise from this analysis. Firstly, the scarcity of Coleoptera is striking, for Dibb (1948) gives a very long list of beetles in his group Limicoles. Of course if the collecting methods of the coleopterist were applied to the mud flat a much longer list of beetles would be made but the flotation method undoubtedly reveals most of the beetle larvae that are present in the samples for they float up very readily. It is suggested that their place in this fauna is preoccupied by Diptera, especially Tipulidae. There is in this deficiency some contrast with the filters for there the 6 small Staphylinid beetles and *C. ustulatus* mentioned above are really quite abundant in their restricted seasons of emergence. Their numbers are masked in the grand totals because they are so few in comparison with the continuously breeding Diptera.

The second surprising fact is the almost total absence in the flotation collections of the insect inhabitants of trees, many of which must fall to the ground either by design or accident. Yet in the flotations no single representative of Lepidoptera, Psocoptera or tree species of Coleoptera has been observed. Nor were any Hemiptera taken apart from an occasional Aphid of tree origin. This must mean that either tree insects falling on the mud leave it quickly or are quickly destroyed by the mud dwelling larvae.

An analysis of the Dipterous larvae and pupae shows that 41 per cent. were Chironomidae; 30·1 per cent. Tipulidae; 16·0 per cent. Psychodidae; 6·8 per cent. Ceratopogonidae; 3·5 per cent. *Dixa*; 0·1 per cent. Mycetophliidae; 0·2 per cent. Ptychopteridae. Trichoceridae were represented by only 4 larvae, while other Diptera formed 1·7 per cent. of the collection. These last were chiefly Empididae, Dolichopodidae and Syrphidae, but these were not dealt with in sufficient detail to warrant any further comment. Tabanidae did not occur but these flies are not seen in the locality.

Indications of the marginal character of the environment may next be considered. Firstly, as in most areas of mud, there is a natural grading in moisture content towards the margin. Secondly, owing to the trampling of animals and similar causes, depressions form which give rise to small transient pools. Thirdly, the moisture content varies with the rainfall both from day to day and over longer periods. Fourthly, it varies in drainage according to the substratum, whether this is pervious or impervious. Mud therefore forms an environment which is graded irregularly between aquatic and terrestrial. Besides being inhabited by forms which are adapted to a life in damp, wet, or saturated silt it is also subject to oviposition by terrestrial forms which normally inhabit humus or rich soil on the one hand and by forms which live in stagnant water on the other hand. Such invaders are much under the influence of subsequent weather conditions and it would be expected that they would occur in smaller numbers than the more natural denizens. Thus the species encountered in such genera as *Limnophila*, *Oxydiscus*, *Molophilus*, *Erioptera*, *Rhypholophus*, *Brillia*, *Prodiamesa*, *Metriocnemus*, *Limnophyes* and *Pericoma* have mostly been represented by many individuals for they are mainly otherwise recorded from such sites as saturated silt or sand, springs, and moss or alga covered stones in streams. On the other hand, species encountered in the large genera *Limonia*, *Dicranomyia*, *Chironomus* and the more nearly terrestrial genera of Orthocladiinae have been met with in very small numbers and in several cases the species is represented by a single record amongst the 11,500 total of larvae. *Chironomus* for instance is a typically aquatic genus and is well represented amongst the flies above the flat but only 4 species of their larvae were floated, 2 represented by 2 individuals each and the others by a single capture. Two species of Trichoptera are fairly prevalent but otherwise this order and Plecoptera are barely represented and no Odonata were taken.

Lloyd (1944) studied the fauna of the mud flat in Gledhow Valley by collecting above it and by breeding in cylinders, and recorded that 44 per cent. of the emerging flies were of the special sewage filter species. The Roundhay sites now under consideration were also studied, but to a lesser extent, and breeding yielded 10 per cent. sewage flies amongst 1150 insects emerging (Lloyd, unpub.). In the present observations the proportion of sewage flies emerging in the breeding cylinders has been much lower than these records. The following members of the association have either been bred, recognised as larvae, or taken over the flat under circumstances that made it reasonably certain they had bred in the mud : *Metriocnemus hygropetricus* (= *longitarsus*), *M. hirticollis*, *Limnophyes minimus*, *Psychoda alternata*, *P. severini*, *P. cinerea* and *Anisopus fenestralis*, and to these Lloyd's previous list adds *Orthocladius perennis*. The Roundhay mud and the Gledhow Valley mud are of very different structure for the former is shallow, tenacious of moisture but well drained, with little surface algae, and it does not become corrupt in the breeding cylinders. That of Gledhow Valley is deep oozy mud, poorly drained, coated with a scum of Cyanophyceae, and becomes very corrupt when removed from a free air supply. It is possible that the latter is more suited to the filter insects, or less suited to their competitors, than the former type.

ACKNOWLEDGEMENTS.

We record our debt to the authorities of the British Museum (Natural History) for identification of the insects collected and reared, especially to Mr. Paul Freeman who has been our frequent correspondent. Mr. W. D. Hincks has kindly dealt with the Coleoptera. We are also grateful to the Leeds University Photographer, Mr. H. Blackledge, for his painstaking help.

SUMMARY.

A survey of the insect fauna of a patch of woodland mud has extended through two years with an attempt at assessing the variety and density of the insects chiefly by flotation. The larvae of Chironomidae, Tipulidae, Psychodidae and Ceratopogonidae are strongly dominant both in variety and numbers. In these prevalent families features of development and general behaviour are recorded and food has been determined by examination of stomach contents. Remarkable features of this fauna are the scarcity of Coleoptera and the variety of habit and adaptive structure noted in Tipulid larvae in so small a space.

Following the theory that the important macrofauna of sewage filters is a derivative of that of the fresh water mud flat, a comparison is made of the features of the two types of environment. The former is characterised as

possessing few species of very great abundance and a scatter of species relatively very rare. The mud flat, however, harbours many species that are abundant, or fairly abundant, in a far less dense association.

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PLATE I.

RESPIRATORY MECHANISM IN TIPULID LARVAE.

FIG. 1.—*Rhypholophus haemorrhoidalis* Zetterstedt.
FIG. 2.—*Molophilus griseus* Meigen.
FIG. 3.—*Ilysia maculata* Meigen.
FIG. 4.—*Erioptera lutea* Meigen.
FIG. 5.—*Gonomyia lucidula* de Meijere.
FIG. 6.—*Elaeophila submarmorata* Verrall.

(Scaled to 0·1 mm.)

PLATE II.

RESPIRATORY MECHANISM IN TIPULID LARVAE.

FIG. 7.—*Pseudolimnophila lucorum* Meigen.
FIG. 8.—*Phylidorea fulvonervosa* Schümmel.
FIG. 9.—Wood-feeding larva, tentative *Epiphragma sp.*
FIG. 10.—*Pilaria nemoralis* Meigen.
FIG. 11.—First Instar, *Phylidora fulvonervosa.*
FIG. 12.—First Instar near moult, *Pilaria sp.*, probably *P. discicollis* Meigen.

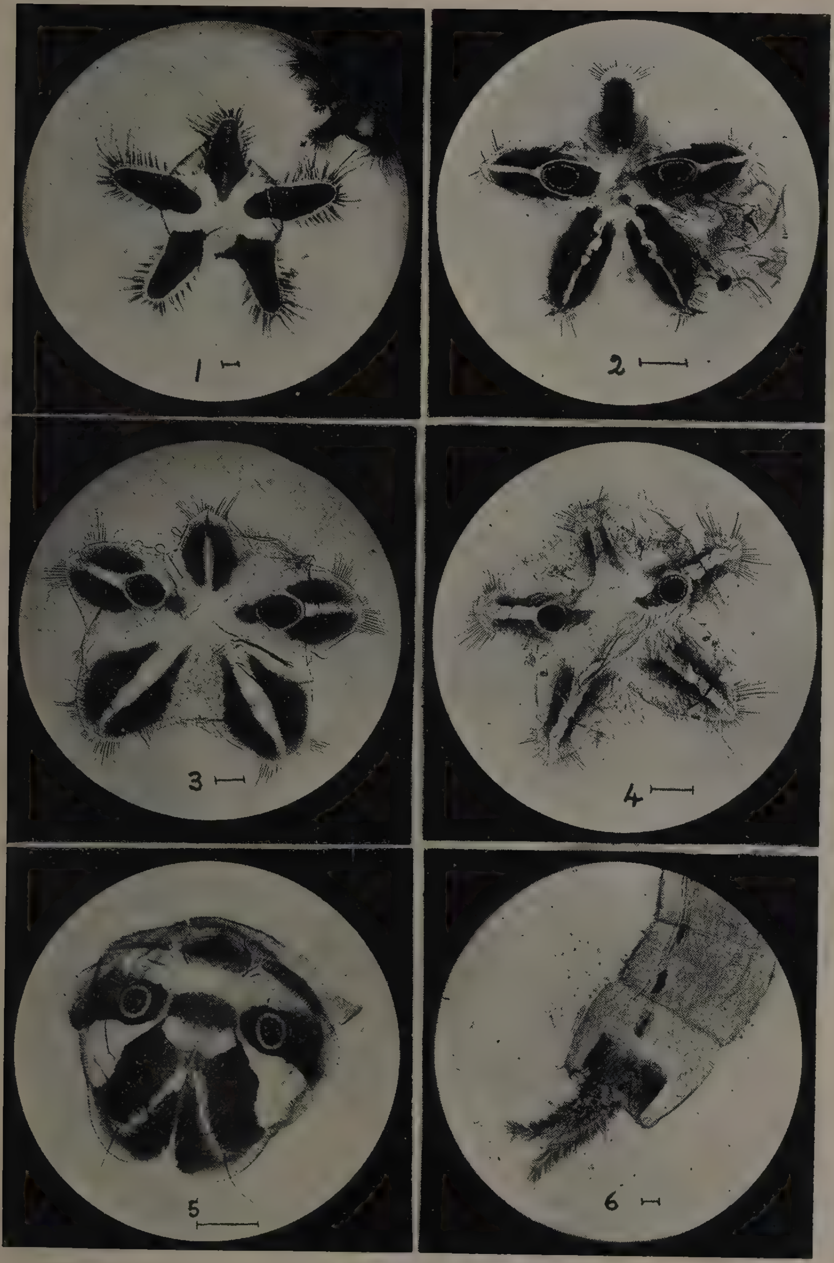
(Scaled to 0·1 mm.)

PLATE III.

HEAD CAPSULES AND FEEDING IN TIPULID LARVAE.

FIG. 13.—Head of half-grown *Pseudolimnophila lucorum* Meigen.
FIG. 14.—Head of *Phylidorea fulvonervosa* Schümmel showing snake-like gape.
FIG. 15.—*Phylidorea fulvonervosa* swallowing Oligochaete worm.
FIG. 16.—*Elaeophila submarmorata* Verrall containing copepod (Harpacticidae).
FIG. 17.—*Oxydiscus senilis* Haliday containing thecate Rhizopods.
FIG. 18—*Pilaria nemoralis* Meigen containing a relatively large Tipulid larva.

(Scaled to 0·1 mm.)



Respiratory mechanism in Tipulid larvae.

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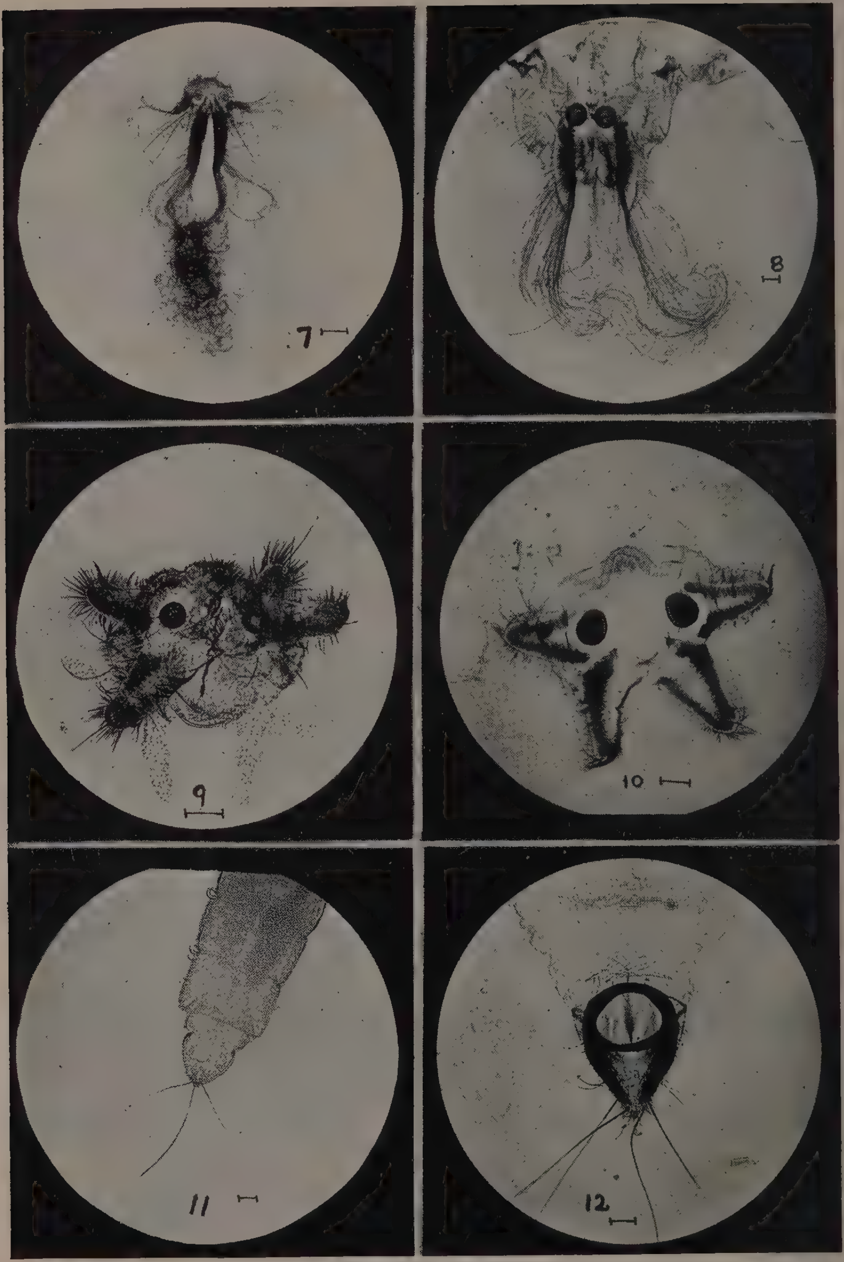

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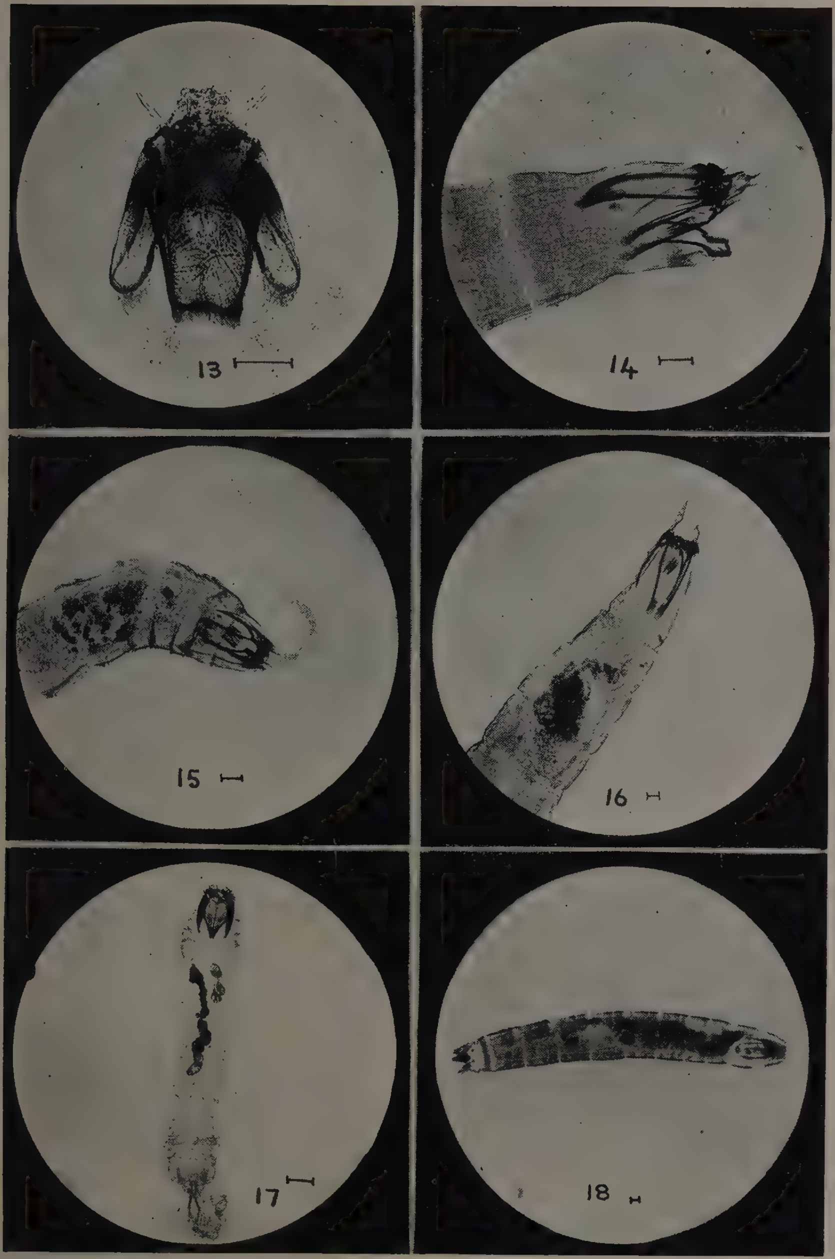
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Head capsules and feeding in Tipulid larvae.

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Vol. 105. Part 14. Pp. 315–353. 22 figs. 15th November, 1954

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ORTHOPTERA-ENSIFERA FROM NORTHERN KENYA AND JUBALAND.

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(*Paris*)

AND

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(*University of Nottingham*).

Manuscript received 31st July, 1953.

(Read 5th May, 1954.)

With 22 Text-figures.

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INTRODUCTION.

THIS paper is a further contribution towards the knowledge of the orthopteroid insects of the region bounded roughly by Lake Rudolf, the River Tana, the River Juba, the Daua Parma and the southern Ethiopian uplands. This large, mainly semi-desert area is described more fully elsewhere (Kevan and Chopard, 1954).

As before, a small number of additional records from the Turkana Desert to the west of Lake Rudolf are also included and references by previous authors to species from the area under review have been incorporated. New species, except for *Peronura samburu* and *Cymatomera excisa*, are attributable to the senior author. The specimens including types are (with the exception of the type of *Acheta zolotarewskyi*, which is in Paris, and those collected by Drs. B. Bezon and F. W. Bræstrup, which are in Copenhagen) in the British Museum (Natural History). Unless otherwise stated, material was collected by the junior author. Localities cited in the text are usually referred to by name only, but details regarding their latitude, longitude, altitude and topography will, in most cases, be found either in the paper dealing with the Blattodea (Kevan and Chopard, *l.c.*) or in that recording the Mantodea (Kevan, 1954); those not listed in either of these papers are given in Part III of the present work.

Of the present series, only the part dealing with the Acrididae remains uncompleted ; those on other Caelifera (Kevan, 1954*a*) and on the Phasmatodea (Chopard and Kevan, 1954) are already in print, and that on the Dermaptera (Kevan, 1954*b*) should appear shortly.*

ACKNOWLEDGMENTS.

Acknowledgment is due, as previously, for the help rendered by the trustees and staff of the Coryndon Memorial Museum, the Keeper of Entomology, British Museum (Natural History), the East African Anti-Locust Directorate (as it then was) and Drs. S. L. Tuxen and F. W. Bræstrup of Copenhagen.

II. DESCRIPTIONS OF AND NOTES ON THE SPECIES.

1. Superfam. GRYLLACRIDOIDEA.

Fam. GRYLLACRIDIDAE.

Stictogryllacris lyrata (Kirby, 1899).

ISIOLO : semi-desert-grass and open acacia-thorn, 3.vi.1946, 1 ♀.
Distribution : East Africa ; described from Zanzibar.

Stictogryllacris pallidus Chopard sp. n.

Type ♂, KENYA, Garissa district : AFWEIN, 00° 17′ N., 39° 22′ E., desert-grass and thorn-bush, 26.i.1944 (*D. K. Kevan*).

A small species of an almost entirely pale yellow coloration. *Head* shining, possessing a brown mark in the shape of an inverted V above ; fastigium verticis as wide as first antennal segment. Face very long, yellow ; clypeus much wider above than below. Antennae and palpi yellow. *Pronotum* transverse with the anterior margin sinuated in the middle, posterior margin truncated, feebly notched in the middle ; disc yellow, shining, with a brown spot in the middle of the anterior part ; anterior sulcus deep ; lateral lobes higher than long, yellow, with inferior margin angulate behind the middle, posterior angle obtuse but not rounded, posterior margin straight as far as the humeral sinus which is rather deep. *Abdomen* yellow ; anal segment rounded, smooth, the posterior margin convex with a small tubercle on each side ; subgenital plate small, transverse, with the posterior margin possessing a narrow notch in the middle ; styli cylindrical. Cerci yellow, rather short, almost straight. *Legs* yellow ; anterior and median tibiae armed with two spines on each superior margin in addition to the apical spurs. Posterior femora rather short and stout, armed, in the apical half of the inferior margin, with five external and four internal spines ; tibiae armed above with five small, brown, internal and six external spines ; external apical spurs rather short, similar to the spines ; internal spurs slender, yellow with brown tips, the inferior one short, the superior one longer, straight. *Elytra* and *wings* transparent with yellowish veins ; elytra widening beyond the middle, with a trifurcate radial vein, *Rs* simple, emerging quite near the base ; *M* united at base with *Cu*, but separated from it a little beyond this, the two branches straight and parallel ; *Cu* not divided, sinuated. Wings with radial vein trifurcate.

Measurements : Length of body, 13 mm. ; pronotum, 2·5 mm. ; posterior femur, 7 mm. ; elytra, 18·5 mm. ; width of elytron, 6·5 mm.

---

* Since proofs were corrected, this has also been published.

Distribution : Known only with certainty from the type locality. [There is, however, a single Turkana male in the Coryndon Museum, Nairobi—recorded by Kevan (1950*a*) as *Gryllacris* sp.—which resembles the new species, but it is damaged and lacks the elytra.—*D. K.*].

Eremus nigrifascies Sjöstedt, 1909.

Mansur (Giglio-Tos, 1917) : Requires confirmation.

Distribution : East Africa.

Ametroides kibonotensis (Sjöstedt, 1909).

Mt. Marsabit : grassy patch near forest, 26.ii.1944, 1 ♀.

Bolívar (1922) records a nymph of *Eremus* sp. from Mt. Nyiro which might conceivably refer to this genus.

Distribution : East African Highlands.

2. Superfam. TETTIGONIOIDEA.

Fam. Phaneropteridae.

The subfamily Phaneropterinae is by far the most fully represented of the Ensifera in the area. This may be due to the fact that large numbers of species feed upon acacias and allied plants which form a very great part of the vegetation of the region under review.

Pseudisotima punctata Schulthess, 1898.

"Girma" (Schulthess, 1898) : type locality. Moyale : sparse bush, 15.vi.1946, 2 ♂, 1 ♀.

Distribution : Previously known only from the type locality. It has been taken also in the Ogaden (El Carre, 05° 51′ N., 42° 06′ E., 3000 ft., scrub, 4.vi. 1947, *D. K. Kevan*) and also occurs in Borana Province, southern Ethiopia.

Euthyphlebia parallela Schulthess, 1898.

Dolo (Schulthess, 1898) : type locality.

Distribution : Known only from the type locality

Epiphlebus crypterius Karsch, 1896.

Samburu district : vi.1944, 1 ♂, 2 ♀ (*E. Opiko*).

Distribution : Previously known only from Somalia.

Epiphlebus ruspolii Schulthess, 1898.

"Ganana" (Schulthess, 1898) : type locality.

Distribution : Endemic to the area.

Peronura somali Schulthess, 1898.

DAMASSA: desert-grass and thorn-bush, 24.v.1947, 1 ♀. LUGH (Schulthess, 1898): type locality.

Salfi (1939) records *P. somali* (?) from Ethiopian MOYALE, but this probably refers to *P. diminuta* sp. n. (p. 319).

Distribution: Known only from the localities mentioned.

Peronura rivae Schulthess, 1898.

DOLO (Schulthess, 1898): type locality. MOYALE: open bush, 15.vi.1945, 1 ♀.

The Moyale specimen differs from the type in the shorter elytra (11·5 mm.) but its coloration, the armature of the legs and the shape of the ovipositor agree fully with the original description.

Distribution: Known previously only from the type locality.

Peronura viridis Chopard sp. n.

Type ♀, KENYA, Isiolo district: BAMBOTA, 00° 20′ N., 38° 20′ E., desert-shrub formation, 6.vi.1946 (*D. K. Kevan*).

Size rather large; green. Fastigium verticis triangular acute at apex, feebly sulcate above; fastigium frontis also triangular with feebly projecting sides and rounded apex. *Face* smooth, green. *Pronotum* a little darkened above; lateral lobes with oblique inferior margin, humeral sinus almost obsolete. *Legs* long, green; anterior femora armed beneath with three posterior spines and seven anterior ones; median femora with eight to ten spines; posterior femora with six external and nine internal spines; all the femoral spines green; genicular lobes with very small spines. *Elytra* extending almost to the apex of the abdomen, rounded at the tips; *Sc* and *R* separated at the base, united a little after the middle, simple; *M* straight, not divided, ending at the internal angle; reticulation between the veins close and irregular. *Ovipositor* short, feebly but regularly curved from the base, its margins rather strongly denticulated. Subgenital plate rounded, weakly notched at the apex, carinated in the middle.

Measurements: Length of body, 25 mm.; pronotum, 7·5 mm.; anterior femur, 13·5 mm.; posterior femur, 31·5 mm.; elytra, 21 mm.; ovipositor, 10 mm.

This species is close to *P. hildebrandtiana* Karsch, 1888, described from Kenya (Mombasa), but differs in the much shorter ovipositor.

Distribution: Known only from the type locality.

Peronura vicina Chopard sp. n. (fig. 1).

Type ♀, KENYA, Marsabit district: CHOPA GOF CRATER, 02° 25′ N., 38° 03′ E., scrubby bushes, 12.vi.1946 (*D. K. Kevan*).

Very close to the last species; larger than *P. viridis* with shorter legs and elytra. *Anterior femora* a little dilated at the apex, feebly armed beneath with one external and three internal spines, median femora with five external and seven internal spines. *Elytra* shorter than those of *P. viridis* but having the same shape and venation. *Ovipositor* a little longer and less strongly curved; subgenital plate in the shape of a V.

Measurements: Length of body, 31 mm.; pronotum, 8 mm.; anterior femur, 12 mm.; median femur, 14·5 mm.; posterior femur (lacking)[1]; elytra, 17 mm.; ovipositor, 13 mm.

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[1] The hind femur of another example of similar dimensions is 27·5 mm. in length.—D. K.

This species differs also from *P. hildebrandtiana* in the shorter ovipositor, the shape of the subgenital plate and the weaker armature of the femora.

Allotype ♂ : Same data as type.

The males of species of the genus *Peronura* have hitherto remained unknown [for certain, although *P. elgonis* Chopard, 1938, the type of which is a male, was tentatively placed in this genus]. The following description is undoubtedly that of the male corresponding with the female above.

Head green with a brown band above and a narrow yellow line at each side. Fastigium verticis very narrow, triangular, sulcate, above separated from the fastigium frontis ; the latter feebly projecting, narrow and rounded at the tip. Face yellow, smooth. *Pronotum* a little widening posteriorly ; lateral lobes much longer than high, with inferior margin oblique and posterior angle much rounded ; humeral sinus visible but not deep. *Abdomen* green, a little darkened above ; tenth tergite projecting, deeply notched at the apex, the lobes so delimited thick, rounded and divided laterally by a deep excision (fig. 1). Subgenital plate very large, curved upwards to join the tergite, divided at the apex into two cylindrical, diverging lobes with rounded apices. Cerci very short, conical, entirely hidden under the tenth tergite. *Legs* long, a little darkened. Anterior and median femora rounded above except for the extreme apex which is compressed and carinated ; anterior femora with infero-anterior margin unarmed, posterior margin armed with four or five small spines, genicular lobes with two very small spines ; tibiae sulcate above, armed with three spines near the apex of the anterior margin above and with twelve spines on each margin beneath ; tympana conchiform. Median femora with four or five spines on each inferior margin ; median tibiae with the same armature as the anterior ones. Posterior femora long and slender, armed on each inferior margin with six or seven very small blackish spines; genicular lobes unspined. *Elytra* rather wide, with parallel margins and rounded apices ; anterior field more than half as wide as the posterior field (2·8 as against 4·2 mm.) ; *Sc* and *R* separated, the former ending on the anterior margin before the apex ; *Rs* emerging before the middle, divided ; *Cu* strongly curved at base, forming a large cubital field which is filled with close, parallel veinlets ; the same close reticulation can be seen in the other fields, chiefly the cubito-median. *Wings* absent.

Measurements : Length of body, 32 mm. ; pronotum, 7 mm. ; anterior femur, 13 mm. ; posterior femur, 32 mm. ; posterior tibia, 35 mm. ; elytra, 26·5 mm. ; width of elytron, 7 mm.

The general aspect of this insect is the same as that of the female from which it differs in the more pronounced humeral sinus and the degree of development of elytra and wings.

[There is some additional material as follows :

CHOPA GOF CRATER : same data as type (taken in same small bush) 3 ♂, 1 ♀.

Distribution : Known only from the above locality.—*D. K.*]

Peronura diminuta Chopard sp. n.

Type (♂) and *Allotype* (♀), KENYA, N. F. D. : MOYALE, open bush, 15.vi.1946. (*D. K. Kevan*).

♂, ♀ : This species is almost an exact repetition of the last on a rather smaller scale. The very peculiar shape of the abdominal extremity is almost exactly the same in both species (cf. fig. 1) ; the venation of the elytra presents no difference. The female subgenital plate is feebly carinated in the middle. The armature of the legs is somewhat weaker, but the number of spines is very variable.

Measurements: Length of body, ♂, 21 mm., ♀, 25 mm.; pronotum, ♂, 5·5 mm., ♀, 6·5 mm.; anterior femur, ♂, ♀, 11·5 mm.; posterior femur, ♂, ♀, 27 mm.; posterior tibia, ♂, ♀, 31 mm.; elytra, ♂, 23 mm., ♀, 18·5 mm.; width of elytron, ♂, 6 mm., ♀, 5·5 mm.; ovipositor, 11 mm.

[Further material is known as follows:

MOYALE: upland grassland and bush, 15.vi.1946, 5 ♂, 2 ♀; cultivation, 8–10.vi.1947, 7 ♂, 3 ♀. YASERE: thorn-bush country, 14.vi. 1946, 2 ♀.

Salfi's (1939) record of *P. somali* (?) from Ethiopian MOYALE doubtless refers to this species.

Distribution: Known only from Moyale but it is possible that the present species represents the more usual form of which *P. vicina* may merely be a large localized subspecies.—*D. K.*]

Peronura trochlearis (I. Bolívar, 1922), **comb. nov.**

Horatosphaga trochlearis I. Bolívar, 1922, *Voy. Rothschild, Afr. or. angl. Anim. Artic.* **1**: 199.

The decision to remove this species from its original genus to the present one was taken on the grounds that it resembles the newly-discovered *Peronura* males very closely, the similarity to *Horatosphaga serrifera* Schaum, 1853, (the type species of its former genus) being less close. The male genitalia (cf. fig. 1) and the venation of the elytra are almost identical with those of *P. diminuta* of which it might almost be taken to be a macropterous form. It is possible that it represents the male of some described species of *Peronura* but, although it has been taken in association with *P. somali*, it is probably rather too small to be that species and for the same reason it would not appear that *P. viridis* is its female. A revision of this group of Phaneropterinae is required since it is very likely that males and females of other heteromorphic species have been described in different genera.

DAMASSA: desert-grass and thorn-bush, 19.xii.1944, 2 ♂. LAK TELANGO: desert-grass and thorn-bush, 26.v.1944, 1 ♂. WAJIR: desert-grass and thorn-bush, 7.i.1945, 1 ♂.

Distribution: Described from "South of Lake Rudolf between the railway and the lake"[2] and known also from Turkana. A common species in the area under discussion, the males being frequently found at light.

Peronura samburu Kevan sp. n. (fig. 2).

Type ♂, KENYA, Samburu: BARSALINGA DRIFT [00° 43′ N., 37° 08′ E.], xi.1946 (*D. N. Hamilton*).

Very similar to the last species from which it differs only in detail, sharing with it an elytral venation similar to that of *P. vicina* and *P. diminuta*; the elytra themselves are longer than in *P. trochlearis* resulting in the main veins being a little more widely spaced at the apex. The costal vein is not darkened as it is in *P. trochlearis*; the pronotum is a little narrower with the disc less strongly pigmented; legs green, not brownish. The spines on the legs are rather more numerous also than in that species which is much the same as *P. vicina* in this respect; anterior femora with infero-anterior margin unarmed, posterior margin with five or six small spines, tibiae with three or four spines on the anterior and about twelve on each of the posterior margins; median femora with nine external and six internal spines, tibiae with eight spines on the superior margin and twelve internal and fourteen external spines on the inferior margin; posterior femora below with eight external and ten internal spines, tibiae with about twenty or more spines on the superior and both inferior margins. Supra-anal plate conforming to the general pattern found in the three preceding species (fig. 1) but differing as illustrated (fig. 2); subgenital plate a little less strongly curved and with less distinctly rounded apices to the rami.

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[2] Presumably in Baringo district, outside the area considered here (*cf.* note in Chopard and Kevan, 1954.)

Measurements: Length of body, 22 mm.; pronotum, 5·5 mm.; posterior femur, 26·5 mm.; elytra 32 mm.; width of elytron, 6·4 mm.

Paratype ♂, KENYA: ISIOLO, 12.i.1937 (*Dr. B. Benzon*) [Copenhagen Museum].

Similar remarks concerning the relationships of this species may be made as for the last.

Distribution: Known only from the places given..

Pantolepta heteromorpha Karsch, 1888.

DAMASSA: desert-grass and thorn-bush, 17.xii.1944, 5 ♂, 1 ♀. MT. MARSABIT: upland grassland near forest, 26.ii.1944, 1 ♀. MOYALE: cultivation, 8–10.vi.1947, 1 ♂, 1 ♀. SAMBURU district: vi.1944, 1 ♀ (*E. Opiko*). YASERE: thorn-bush country, 14.vi.1946, 1 ♂, 1 ♀.

Distribution: British East Africa, Ethiopia; described from Mombasa. One of the commonest species of Phaneropterinae in the area, the males being very frequent at light.

Plegmatoptera hoehneli Brunner v. W., 1891.

CHOPA GOF CRATER: scrubby bushes, 13.vi.1946, 1 ♀.

Distribution: Described from Kilimanjaro and known from several localities in other parts of East Africa.

Horatosphaga serrifera Schaum, 1853.

CHOPA GOF CRATER: scrubby bushes, 13.vi.1946, 2 ♀.

Distribution: Described from Portuguese East Africa (Mozambique).

Isotima reticulosa Karsch, 1888.

YASERE: thorn-bush country, 14.vi.1946, 1 ♀.

Distribution: East Africa; described from Mombasa.

Tropidonotacris Chopard gen. n. (fig. 3).

A genus very remarkable on account of the head and pronotum, which are rather strongly carinated.

Fastigium verticis subacute; lobes of meso- and metasterna short, angular and with rounded apices. Anterior tibiae with oval tympana, supero-external margin armed with a few spines; coxae unarmed. Elytra long and rather wide; *Sc* and *R* separated, *R* bearing three branches. Wings a little longer than the elytra. Subgenital plate of the male divided, without styles.

Type species : Tropidonotacris carinatus sp. n.

This new genus is rather difficult to place in the Phaneropterinae but it seems that it must be assigned to the Ducetiae.

Tropidonotacris carinatus Chopard sp. n. (fig. 3).

Type ♂, Kenya, Mandera district : Takabba, 03° 25′ N., 40° 12′ E., thorn-bush, 11.xii.1944 (*D. K. Kevan*).

Rather large ; green. *Head* (fig. 3*a*) carinated above ; fastigium verticis projecting above the fastigium frontis in a point rounded at the apex ; fastigium frontis very narrow, only slightly projecting. Face very long. Eyes rounded. Antennae slender. *Pronotum* (fig. 3*a*) strongly carinated throughout its whole length ; anterior margin angulated ; posterior margin strongly convex ; lateral lobes with rounded insertion as high as long, with anterior angle a little more than 90° ; inferior margin oblique ; posterior angle and margin rounded ; humeral sinus visible but not deep. *Abdomen* slightly carinated in the middle above ; tenth tergite transverse with straight posterior margin and a somewhat depressed middle ; supra-anal plate small, triangular, acute at apex. Subgenital plate large with sinuated margins, narrowing at apex, deeply divided but the lobes contiguous to the apex (fig. 3*b*) ; styles absent. Cerci rather stout, shorter than the subgenital plate, feebly curved, a little flattened towards the apex which ends in a sharp point. *Legs* rather long, green. Anterior coxae without a spine. Anterior and median femora armed beneath with a dozen rather strong spines on the anterior margin, one or two only on the posterior margin ; genicular lobes armed with two very small spines ; tibiae sulcate above, armed beneath with six or seven spines on each margin ; anterior tibiae with an oval tympanum on either side. *Elytra* much longer than the abdomen, rather wide, the greatest width being at about one-third of the length from the base ; anterior field at the base about half as wide as the posterior field at its greatest width (4·0 as against 7·5 mm.) ; anterior margin strongly convex at base ; apex rounded ; *Sc* and *R* separated, rather strongly sinuated ; *R* giving off three branches ; left anal field brown with a very thick anal vein ; right anal field transparent. The background of the elytra occupied by a double reticulation, there being a very tiny, irregular one and a wider one formed by the transverse veinlets. *Wings* extending a little beyond the elytra, with a greenish anterior margin ; apical triangle well developed.

Measurements : Length of body, 17 mm. ; pronotum, 4·5 mm. ; posterior femur, 17·6 mm. ; elytra, 31 mm. ; width of elytron 10·5 mm.[3]

[Further material is known from the following localities :

Afwein : desert-grass and thorn-bush, 26.i.1944, 5 ♂. Banissa : thorn-bush country, 10.xii.1944, 1 ♂. El Katuio : desert-grass and thorn-bush, 16.vi.1944, 3 ♂. Janju : desert-grass and thorn-bush, 22.i.1944, 7 ♂. Muddo Gashi : desert-grass and thorn-bush, 20.i.1944, 4 ♂.

Distribution : In addition to the localities mentioned the new species has also been observed in Turkana and Somalia (though no specimens from these territories were collected). It is one of the commonest members of the subfamily to come to light in these regions. The females are seldom so attracted and only one has ever been observed ; it eluded capture, but resembled the males closely.—*D. K.*]

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[3] The total width does not agree with the combined width of the anterior and posterior fields because the greatest width of each is not situated at the same place on each elytron.

Ducetia punctipennis (Gerstaecker, 1869).

DAMASSA: desert-grass and thorn-bush, 17.xii.1944, 1 ♂. TAKABBA: thorn-bush country, 13.xii.1944, 1 ♂. YASERE: thorn-bush country, 14.vi.1946, 1 ♀.

Distribution: East Africa; described from Zanzibar.

Phaneroptera[4] *nana* Charpentier, 1853.

AFWEIN: desert-grass and thorn-bush, 6.i.1944, 1 ♀. ALGADA AREA: "Nyika" bush, 4.x.1947, 1 ♂. CHEBELE: Tana River bush, xii.1945, 1 ♀ (*J. Adamson*). "GIRMA" (Schulthess, 1898). JANJU: desert-grass and thorn-bush, 24.i.1944, 1 ♂. SAMBURU district: vi.1944, 1 ♀ (*E. Opiko*).

Distribution: Almost the whole of Africa. One of the commonest species in East Africa to come to light.

Phaneroptera punctulata Burr, 1900.

BURA: Tana River bush, 16.i.1944, 1 ♀.

Distribution: Described from Somaliland, this species has recently been recorded from Kenya (Kevan, 1950).

Phaneroptera reticulata Brunner v. W., 1878 (fig. 4).

Although this species was described from quite a different region (Grahamstown, Cape Province, South Africa), the insect below agrees perfectly with Brunner's description in the almost transparent elytra covered with a net of green veinlets in which the principal veins are lost. The supra-anal plate is rectangular with rounded angles; the subgenital plate is long, narrowing at the apex and deeply notched. The cerci are rather long and crossed beneath the subgenital plate; they are somewhat depressed at the apex, ending in a small tooth (fig. 4).

MARSABIT: Upland grassland, 26.ii.1944, 1 ♂.

Distribution: It has previously been suggested (Kevan, 1950) that this species occurs in East Africa; the distribution is perhaps more or less continuous from the eastern Cape Province.

Phaneroptera acaciae Chopard sp. n. (fig. 5).

Type ♂, KENYA, Mandera district: RAHMU, 03° 55′ N., 41° 14′ E., thorn-bush, 19.vi.1944 (*D. K. Kevan*). *Allotype* ♀, KENYA, N. F. D., MANDERA, 03° 57′ N., 41° 52′ E., desert-grass and thorn-bush, 28.xii.1944 (*D. K. Kevan*).

♂. Small, green, punctuated with brown. Fastigium verticis narrow triangular, feebly sulcate, separated from the fastigium frontis. *Eyes* globular, projecting; lateral ocelli large. *Pronotum* flat above; anterior margin straight, posterior margin rounded; lateral lobes as long as high, their insertion on to the disc rounded; humeral sinus well defined but not deep. *Abdomen* with tenth tergite transverse with a straight posterior margin; supra-anal plate large, rectangular, with a slightly concave apical margin; subgenital plate very long, deeply notched, the lobes much lengthened and with parallel margins (fig. 5). Cerci shorter than the subgenital plate, rather stout, slightly curved and with the apex ending in a small tooth. *Legs* rather short, spotted with small rufous brown specks; all the femora without apical spines. Anterior coxae each armed with a short, blunt spine; anterior tibiae sulcate above, armed with a single anterior spine, unarmed beneath; tympana oval. *Elytra* rather wide at base then rapidly narrowing, the apex very narrow; *Sc* and *R* separated, straight; *Rs* furcate, mirror rather large, round; cubital field darkened; anterior field transparent with strong, rather regular veins; remainder of the elytron with close reticulation, the small meshes between the veinlets brown.[5] *Wings* longer than the elytra.

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[4] For a discussion of this generic name, see Roberts (1941).

♀. Similar to the male; a little larger. *Ovipositor* rather short, much compressed, wide, with the superior margin smooth; inferior margin finely crenulated, apex feebly acute. Subgenital plate triangular. *Elytra* narrower than in the male, with posterior field completely brown, the reticulation standing out in a light colour.

Measurements: Length of body, ♂, 9 mm., ♀, 12·5 mm.; pronotum, ♂, 3·4 mm., ♀, 3·5 mm.; posterior femur, ♂, 13 mm., ♀, 15 mm.; elytra, ♂, 12 mm., ♀, 16·5 mm.; ovipositor, 6·3 mm.

The shape of the elytra is rather different from that of other species of *Phaneroptera*, the base being very much widened and the cubito-anal field somewhat prominent. The male looks rather like a species of the genus *Pyrrhicia* Stål, 1873, but the anterior coxae are feebly armed and, in the female, the shape of the ovipositor is quite different.

[A further specimen is known as follows:

DAMASSA: desert-grass and thorn-bush, 17.xii.1944, 1 ♀.

Distribution: Known only from the localities mentioned.—*D. K.*]

Melidia laminata Chopard sp. n. (fig. 6).

Type ♂, KENYA, Wajir district: EL KATULO, 02° 28′ N., 40° 38′ E., desert-grass and thorn-bush, 16.vi.1944 (*D. K. Kevan*).

Paratype ♂, : Same data as type.

Small, yellow-green or pale green. Fastigium verticis triangular with large and projecting ocelli at the base; fastigium frontis very narrow, somewhat tuberculate. *Pronotum* flat above with a feebly concave anterior margin and a convex posterior one; insertion of the lateral lobes on to the disc subangulate and ornamented with a fine yellow line; lateral lobes as long as high, with the inferior margin rounded and a moderately deep humeral sinus. *Abdomen* green; tenth tergite with a straight posterior margin; supra-anal plate small, triangular; subgenital plate very long and deeply divided into two narrow, parallel plates; styles absent (fig. 6). *Legs* rather long, green. Anterior coxae armed with a short spine; anterior femora armed with two or three very small spines at the apex of the infero-internal (anterior) margin; genicular lobes armed with a very small spine; tibiae distinctly widening above the tympana, sulcate above and without spines; tympana oval. Median femora armed similarly to the anterior. Posterior femora with unarmed margins or with only a very small spine; genicular lobes armed. *Elytra* relatively wide, with convex anterior margins and rounded apices; width of anterior field a little more than half the width of the posterior field (1·6 as against 2·7); *Sc* and *R* separated along their entire length; *R* twice furcate; *Rs* emerging from the middle divided very near to the base. *Wings* longer than the elytra.

Measurements: Length of body, 10 mm.; pronotum, 2·5 mm.; posterior femur, 12·5 mm.; elytra, 16·5 mm.; width of elytron, 4·3 mm.

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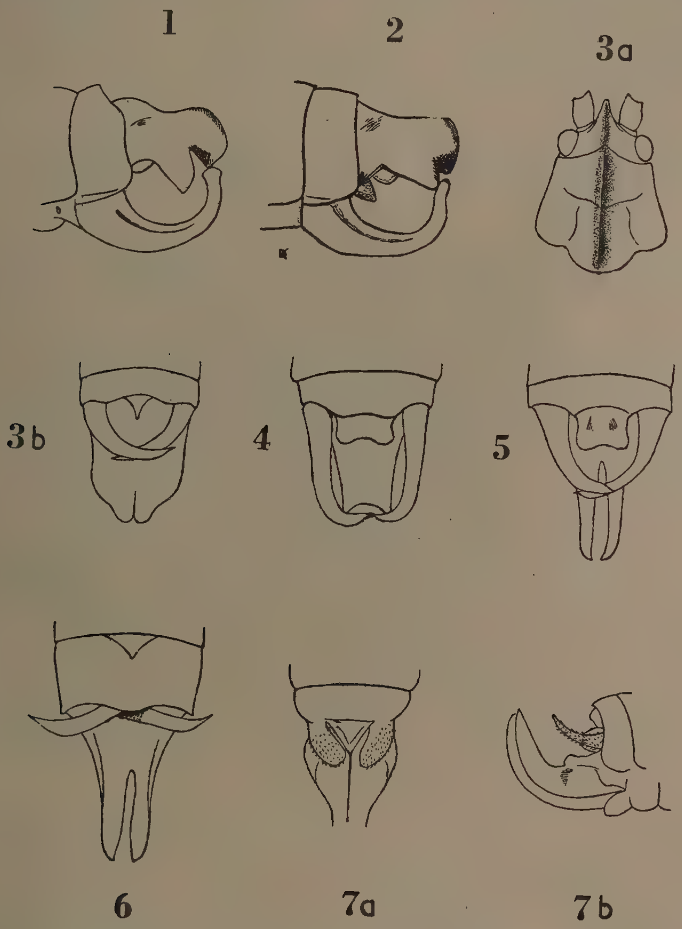
[5] In life the insect gives the impression of being dirty grey-green, scattered all over with blackish points; the dorsum of the abdomen is chestnut-coloured and the whole dorsal aspect of the insect at rest is dark brown.—D. K.

This species has rather the appearance of *Ph. reticulata*, but with wider elytra.

[The elytra are more yellow-green in colour than in other species and usually have a characteristic brown patch at the base of the anal field in the male. The female (data below), which has not been examined by the senior author, lacks this mark but otherwise resembles the male closely in general appearance although it is larger.



FIGS. 1–7.—(1) *Peronura vicina* Chopard sp. n. Apex of male abdomen (lateral) (*P. diminuta* Chopard sp. n. and *P. trochlearis* (Bol.) similar). (2) *P. samburu* Kevan sp. n. Apex of male abdomen (lateral). (3) *Tropidonotacris carinatus* Chopard gen. et sp. n. (*a*) Head and pronotum; (*b*) subgenital plate and cerci of male. (4) *Phaneroptera reticulata* Br. v. W. Subgenital plate and cerci of male. (5) *Phaneroptera acaciae* Chopard sp. n. Apex of male abdomen. (6) *Melidia laminata* Chopard sp. n. Apex of male abdomen. (7) *Melidia kenyensis* Chopard sp. n. (*a*) Subgenital plate of female; (*b*) ovipositor.

The armature of the femora in the female is as in the male ; the female is very similar to that of the next species, but has not the lateral lobes at the apex of the abdomen. The single known example has the following measurements :

Measurements : Length of body, 13·5 mm. ; elytra 19 mm. ; width of elytron 5·2 mm. ; length of hind femur, 14·4 mm. ; ovipositor, 5 mm.

The following material is known in addition to the type :

DAMASSA : desert-grass and thorn-bush, 17.xii.1944, 1 ♂, 1 ♀ (described above) ; 20.xii.1944, 1 ♂. EL KATULO : same data as type, 1 ♂. JANJU : desert-grass and thorn-bush, 22.i.1944, 2 ♂.

Distribution : Known only from the above localities.—*D. K.*]

Melidia kenyensis Chopard sp. n. (fig. 7).

Type ♀, KENYA, Moyale district : YASERE, 30° 30′ N., 38° 55′ E., thorn-bush, 14.vi.1945 (*D. K. Kevan*).

Size medium, green, spotted with small rufous specks. Fastigium verticis very narrow, feebly furrowed above, separated from the fastigium frontis which is slightly tuberculate ; ocelli large, at base of fastigium verticis. *Eyes* projecting, rounded. *Antennae* slender, green. *Pronotum* slightly narrowing in front, flat above, slightly spotted with rufous ; posterior margin somewhat projecting but truncate in the middle and with rounded angles ; insertion of the lateral lobes on to the disc of the pronotum rounded ; lateral lobe a little shorter than high with a feebly sinuate anterior margin, a convex posterior margin and a shallow humeral sinus. *Abdomen* spotted with reddish ; subgenital plate small, triangular with two rounded, pubescent lateral lobes which seem to be dependent from the eighth abdominal sternite (fig. 7*a*). Ovipositor rather short, compressed, abruptly curved, with denticulate margins and the surface covered with small tubercles ; the base of the superior valve strongly swollen (fig. 7*b*). *Legs* rather long. Anterior coxae armed with a rather long spine ; anterior and median femora armed with a small spine near the apex of the anterior margin beneath ; genicular lobes armed with a very small spine ; tibiae sulcate, without spines above ; anterior tibiae with three spines on each side beneath, median tibiae with four ; foramina oval. Posterior legs wanting.[6] *Elytra* rather wide, with almost parallel margins and rounded apices ; anterior field wider than half of the posterior one (2·5 as against 4 mm.). *Sc* and *R* feebly separated, sinuated after the middle so that the greatest width of the posterior field is beyond the middle ; *R* furcate near the apex ; *Rs* merging beyond the middle, furcate. *Wings* slightly exceeding the elytra and with a well-defined apical triangular field ; radial field relatively wide, the radial vein trifurcate.

Measurements : Length of body, 14 mm. ; pronotum, 4 mm. ; elytra, 23·5 mm. ; width of elytron, 6·5 mm. [hind femur, 16·5 mm. ; ovipositor, 5·5 mm.].

This species is very close to the preceding one but larger and remarkable for the shape of the subgenital plate.

[*Distribution :* Known only from the type locality. A further female is also known having the same data as the type.—*D.K.*]

Terpnistria tuberculata Chopard sp. n. (fig. 8*a*).

Type ♂, KENYA, N.F.D. : GARISSA, desert-grass and thorn-bush, 5.i.1946 (*D. K. Kevan*).

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[6] Detached in transit only ; the armature consists only of two small external spines near the apex.—D. K.

A small species; green varied with white. *Head* green; occiput strongly convex; vertex sloping, fastigium verticis wider than the first segment of the antenna, not sulcate, continuous with the fastigium frontis; forehead carinated on the sides. Eyes strongly projecting. Antennae very slender, feebly annulated with brown. *Pronotum* with anterior, margin angulate and upwardly directed, posterior margin elevated in the middle in the form of a large rounded tubercle; lateral keels visible in front and posteriorly, strongly arcuate, white; lateral lobes higher than long with inferior margin rounded, white, posterior part swollen; humeral sinus very distinct, acute. *Abdomen* greenish, smooth; tenth tergite (fig. 8*c*) produced into a long, rectangular plate with parallel, bordered margins, notched apex and the median line elevated in a high carina. Cerci as long as the tenth tergite, thick at the base, then compressed and ending in a plate-like expansion, rounded at the apex. Shape of subgenital plate impossible to describe since damaged. *Legs* varied with white and green. Anterior coxae armed with a rather strong spine. Anterior femora short and stout, a little enlarged at the apex, armed with two spines on the infero-internal margin; tibiae flat above, a little enlarged at the apex; both foramina oval in shape; tibiae armed beneath with four or five small spines on each margin. Median legs lacking. Posterior femora short and stout, armed with four small spines towards the apex of the external margin, the internal margin bearing only one or two very small spinelets. Tibia armed on the superior margin with spines of which some are lamellate, the first two of these being in the form of rounded lobes, the third also strongly lobate, the fourth and fifth less strongly so and the sixth to the ninth of normal shape; the first three spines on the internal margin triangular, the fourth feebly enlarged and the fifth to the ninth normal; beneath, the armature is composed of about fifteen small spines on each margin. *Elytra* green with veins margined white; anterior margin rather strongly convex from the base to the apical third, then parallel to the internal margin which is quite straight; apex slightly truncated; *Rs* ending in the internal angle; *M* unbranched and united with *Rs*; anterior field almost as wide as the posterior field, with few veinlets forming wide areolae. *Wings* with anterior field greenish towards the apex; apical triangle short but wide with numerous veins (fig. 8*b*); radial field widening towards the apex; *R* giving off one branch only; *Cu* thickened and curved, sending off numerous oblique, parallel branches towards the median vein and the apical triangle.

Measurements : Length of body, 13 mm.; pronotum, 3·2 mm.; posterior femur, 9·5 mm.; posterior tibia, 9·5 mm.; elytra, 17·5 mm.; wings, 19 mm.

This species is much smaller than the South African *T. lobulata* Stål, 1876; the posterior tubercle of the pronotum is rounded and the lateral keels not crenulated.

Distribution : The type is unique.

Diogena fausta (Burmeister, 1838).

This species seems to vary rather in respect of the prominence of the lateral keels of the pronotum; these are much more voluminous in some specimens than in others and, generally, more so in males than in females. However, the number of individuals in collections is not sufficient to determine the importance of this variation.

HAGADERA : desert-grass and thorn-bush, 8.i.1946, 1 ♂. MUDDO GASHI : desert-grass and thorn-bush, 15.vi.1944, 1 ♂. RAHMU : desert-grass and thorn-bush, 19.vi.1944, 1 ♀.

Distribution : Egypt to Mauritania and widely distributed in the semi-desert regions south of the Sahara.

Diogena denticulata Chopard sp. n.

Type ♀, Kenya, N.F.D. : El Wak, desert-grass and thorn-bush, 5.xii.1944 (*D. K. Kevan*).

General aspect as in *Diogena fausta* but larger. *Head* greenish with two yellow lines behind the eyes. Fastigium verticis rather wide, a little truncated at the apex, feebly sulcate above. Face green with two callose yellow lines from the eye to the clypeus. *Pronotum* green with a black line along the posterior margin ; anterior margin elevated in a triangular point ; posterior margin acute in the middle ; lateral tubercles massive, a little compressed at their upper extremities, irregularly truncated ; lateral lobes (as in *D. fausta*) with a slightly callose yellow band and three elevated points of the same colour. *Subgenital plate* triangular, a little rounded at the apex. *Legs* with armature similar to *D. fausta* but the foliaceous spines of the posterior legs much wider, the two last spines of the posterior femora contiguous. *Elytra* strongly widening in the middle, their apical margins relatively very long, truncated ; *Sc* and *R* strongly sinuated beyond the middle.

Measu ements : Length of body, 25·5 mm. ; pronotum, 7 mm. ; posterior femur, 21 mm. ; elytra, 39 mm. ; width of elytron, 6 mm. ; ovipositor, 5·6 mm.

This large and beautiful species differs from *D. fausta* in the acutely prolonged anterior margin of the pronotum and the very large lobes of the posterior legs and in the shorter, less acute subgenital plate.

[*Distribution :* Known only from El Wak. A further female is known from this locality, 6.ii.1944.—*D. K.*]

Dioncomena superba Karsch, 1888.

Chopa Gof Crater : Scrubby bushes on crater rim, 13.vi.1946, 1 ♂.

Distribution : East Africa. This species is not uncommon in certain localities and is, in life, most resplendent, the metallic gold, green and purple coloration of the tegmina in particular being very striking in brilliant sunshine in which the insect will fly. This diurnal habit is unusual among Phaneropterinae.

Tylopsis[7] *bilineolata* (Serville, 1839).

Moyale (Ethiopian) (Salfi, 1939).

Distribution : Southern and eastern Africa. A very common species in East Africa, particularly where long grass is plentiful.

Tylopsis dispar Sjöstedt, 1909.

Isiolo : 19.i.1937, 1 ♀ (*Dr. B. Benzon*).

Distribution : East Africa.

Tylopsis gracilis Chopard sp. n.

Type ♂, Kenya, Mandera district : Damassa, 03° 09′ N., 41° 20′ E., desert-grass and thorn-bush, 19.xii.1944 (*D. K. Kevan*).

Small and slender ; testaceous with a dark brown band extending from the head on to the pronotum. Fastigium verticis very narrow, compressed, separated from the fastigium frontis. *Eyes* elliptical, dorso-ventrally lengthened. *Antennae* brown on the external surface. *Pronotum* flat above, the sides somewhat divergent in front; posterior margin truncated; lateral lobe almost twice as long as high, with a sinuated inferior margin and a much rounded posterior angle; insertion upon the disc indicated by a yellow, somewhat callose line. *Abdomen* adorned with a longitudinal brown band on each side; tenth tergite transverse with a feebly concave posterior margin; supra-anal plate almost square, with a convex posterior margin; subgenital plate long, a little widening at the apex, angularly notched. Cerci a little longer than the subgenital plate, feebly curved, ending in a small brown spine. *Legs* long and slender, spotted with brown. Anterior and median femora unarmed beneath, with genicular lobes prolonged into a long point. Anterior tibiae armed above with five or six small spines on the external margin and two spines on the internal margin, with five or eight spines beneath; tympana slit-like. Dorsal armature of the median tibiae similar to that of the anterior ones; beneath, with ten or eleven spines. Posterior femora very slender. *Elytra* very narrow, almost transparent, with a few small brown spots; *Sc* and *R* distinctly separated; *Rs* and *M* furcate. *Wings* much longer than the elytra, spotted with brown in the anterior field. Cubito-anal field of the left elytron brown with light veins.

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[7] For discussion on this generic name see Roberts (1941).

Measurements: Length of body, 11·5 mm.; pronotum, 2·9 mm.; posterior femur, 18·5 mm.; elytra, 16 mm.; wings, 22·5 mm.

This distinctive species may be recognised by its very small size and by the feebly curved cerci which are not at all sinuated.

Distribution: Known only from the type locality.

Eurycorypha varia Brunner v. W., 1891.

Bardera (Giglio-Tos, 1917): Identified with doubt. "Daua" (Schulthess, 1898). Yasere: Thorn-bush country, 14.vi.1946, 1 ♂.

Whether, in view of the large number of species in this genus, Schuthess' determination is reliable is open to question, but there is no valid reason to consider it erroneous since the species is common in East Africa.

Distribution: East Africa, including Turkana. Males are very frequently attracted to light.

Eurycorypha meruensis Sjöstedt, 1909.

This species is very characteristic in the shape of the abdominal extremity.

El Wak: desert-grass and thorn-bush, 5.xii.1944, 1 ♂. Finno: desert-grass and thorn-bush, 17.vi.1944, 1 ♂. Isiolo: iii.1944, 1 ♀ (*J. Adamson*). Moyale: open bush, 15.vi.1946, 2 ♂. Rahmu: desert-grass and thorn-bush, 19.vi.1944, 1 ♀.

Distribution: Described from Kilimanjaro and known also from Turkana. It is a common species in East Africa, coming readily to light.

Eurycorypha kevani Chopard sp. n. (fig. 9).

Type ♂, Kenya, N.F.D.: Mandera, desert-grass and thorn-bush, 7.xii. 1944 (*D. K. Kevan*).

General aspect and size of the preceding species; green. *Head* and *pronotum* coarsely punctured. *Elytra* with anterior margin almost straight; *R* divided near the apex; *Rs* emerging a little beyond the middle, furcate; *M* unbranched. *Wings* extending a very little beyond the elytra. *Tenth abdominal tergite* transverse, with straight posterior margin; supra-anal plate triangular, completely concealed beneath the tergite; subgenital plate long, narrowing towards the apex and very deeply divided into two long narrow lobes which resemble styles (fig. 9). Cerci rather long, feebly curved, acute at apex.

Measurements : Length of body, 15 mm. ; pronotum, 4·7 mm. ; posterior femur, 12·5 mm. ; elytra, 25 mm. ; width of elytron, 8 mm.

The new species is readily distinguished from all others by the shape of the abdominal extremity of the male.

[Additional material is known as follows :

Birchika : desert-grass and thorn-bush, 20.vi.1944, 1 ♂ ; 7.xii.1944, 1 ♂; 8.xii.1944, 2 ♂. Muddo Gashi : 20.i.1937, 2 ♂ (*Dr. B. Benzon*) ; desert-grass and thorn-bush, 1.vi.1944, 1 ♂. Rahmu : desert-grass and thorn-bush, 19.vi.1944, 1 ♂, 1 ♀. Wonte Goda : desert-grass and thorn-bush, 14.xii. 1944, 1 ♂.

The female has not been seen by the senior author. It resembles the male closely and, like it, differs from the last species in the shorter elytra which are less tapering at the apex ; the glaucous green colour (in both sexes), resembling foliage with a waxy bloom, is characteristic, particularly in life. The ovipositor is shorter and more strongly curved than in *E. meruensis* or *E. varia.*

Length of body, 19 mm. ; pronotum, 4·8 mm. ; posterior femur, 13 mm. ; elytra, 26·8 mm. ; width of elytron, 9·5 mm. ; length of ovipositor, 5·5 mm.

Distribution : Known only from the area under discussion, but one of the commonest Tettigonioids coming to light where there are abundant Acacia-trees and bushes.—*D. K.*]

Eurycorypha simillima Chopard sp. n. (fig. 10).

Type ♂, Kenya, North Turkana : Lokitaung, [04° 18′ N., 35° 45′ E.], v. 1945 (*M. Wright*).

Close to the preceding species from which it differs in the shape of the cerci and of the subgenital plate. Cerci stouter and a little sinuated ; subgenital plate with the divided part shorter, the lobes so formed being less slender and somewhat pyriform (fig. 10).

Measurements : length of body, 19 mm. ; pronotum, 5·2 mm. ; posterior femur, 12·5 mm. ; elytra, 25·5 mm. ; width of elytron, 8·5 mm.

[*Distribution :* Known only from the type locality. This species has not been taken in the area under review, but being new to the Turkana fauna, it is included here.—*D. K.*]

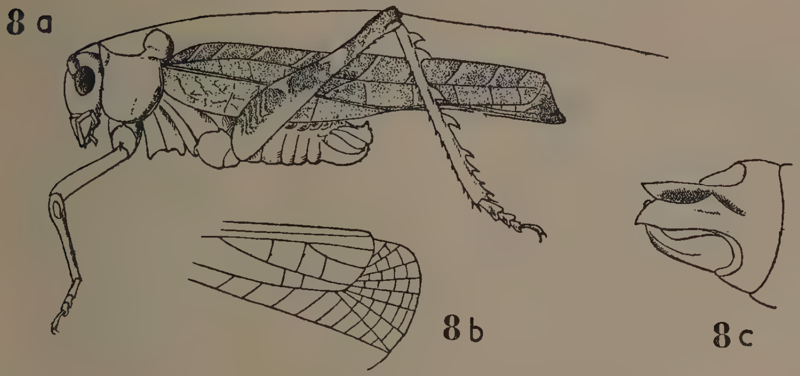
Plangiodes Chopard gen. n. (fig. 11).

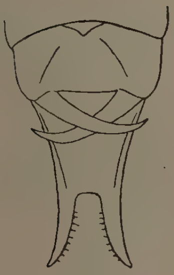
Type species : *Plangiodes carinatus* sp. n.

The species for which the new genus is erected possesses the characters of the genus *Plangia* Stål, 1873, but the forehead is strongly carinated laterally.

Plangiodes carinatus Chopard sp. n. (fig. 11).

Type ♂, Kenya, Garissa district : Afwein, 00° 17′ N., 39° 22′ E., desert-grass and thorn-bush, 26.i.1944 (*D. K. Kevan*).





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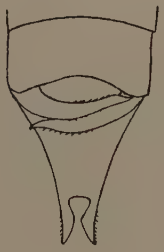

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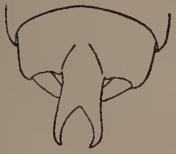

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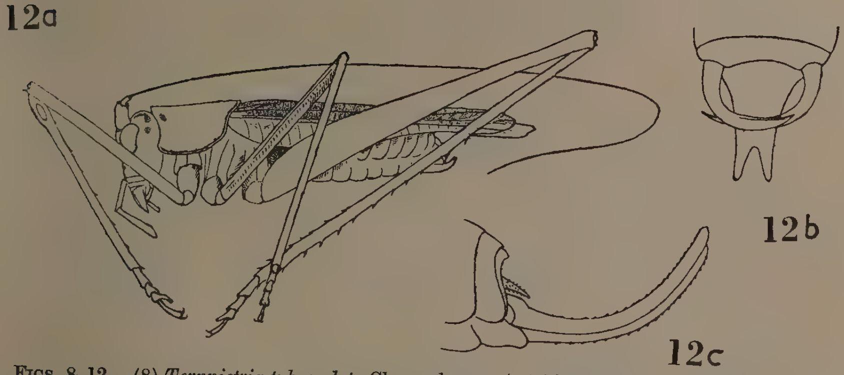


FIGS. 8–12.—(8) *Terpnistria tuberculata* Chopard sp. n. (*a*) Male (type); (*b*) apex of wing of same; (*c*) supra-anal plate and cerci of same. (9) *Eurycorypha kevani* Chopard sp. n. Subgenital plate and cerci of male. (10) *Eurycorypha simillima* Chopard sp. n. Subgenital plate and cerci of male. (11) *Plangiodes carinatus* Chopard sp. n. Supra-anal plate of male. (12) *Kevaniella bipunctata* Chopard gen. et sp. n. (*a*) Male (type); (*b*) apex of male abdomen (dorsal); (*c*) ovipositor.

Compressed, green, having the general appearance of a species of *Eurycorypha*. *Head* a little wider than pronotum ; fastigium verticis scarcely wider than the first antennal segment, sulcate above, truncated at the apex, separated from the fastigium frontis by a deep furrow ; the latter rather wide and rounded ; forehead flat, with a very distinct, longitudinal, yellow carina on either side. *Eyes* elliptical, lengthened dorso-ventrally, projecting. Antennae very slender. *Pronotum* flat above, smooth ; anterior margin a little concave ; posterior margin rounded, bordered yellow ; insertion of lateral lobes on to disc of pronotum almost angular, somewhat concave, finely lined with yellow ; lateral lobes higher than long with the anterior angle somewhat obtuse, the posterior margin very widely rounded and the humeral sinus deep. *Abdomen* green, tenth tergite bearing a downwardly directed plate-like process, very deeply notched at its apex (fig. 11) ; subgenital plate rather short, bearing two small styles. Cerci short and rather stout, curved, ending in a small tooth. *Legs* green, somewhat spotted with white. Anterior femora short, with the anterior margin armed with three small spines ; anterior tibiae quadrangular, each bearing two oval tympana beyond which the tibiae narrow abruptly, inferior margins each armed with seven spines. Median legs a little longer than the anterior ones, femora with similar armature, tibiae a little dilated at the base, armed beneath with about ten spines. Posterior femora thick at base but very slender in the apical third ; external face a little rugose ; inferior margin armed with four small spines towards the apex ; tibiae quadrangular, armed above with sixteen or seventeen spines and beneath with fourteen or fifteen. *Elytra* wide with the anterior margin concave, the internal margin being oblique from the end of the cubital field to the apex which is rounded ; anterior field equalling, at its greatest width, more than half that of the posterior field (3·1 as against 5 mm.) ; *R* and *Sc* contiguous, *R* being separated only a little before the apex, terminating at the internal margin ; *Rs* emerging shortly after the middle, furcate ; *M* curved, simple ; the whole surface of the elytra finely reticulated. *Wings* a little longer than the elytra.

Measurements : Length of body, 14·5 mm. ; pronotum, 3·9 mm. ; posterior femur, 13 mm. ; elytra, 23 mm. ; width of elytron, 7·5 mm.

This species has the appearance of a species of *Eurycorypha* but it cannot be ascribed to that genus owing to its narrow fastigium verticis.

[A further example is known as follows :

BIRCHIKA : desert-grass and thorn-bush, 7.xii.1944, 1 ♂.

Distribution : Known only from the two localities mentioned—*D. K.*]

Kevaniella Chopard gen. n. (fig. 12).

General shape rather slender with long legs. Fastigium verticis very narrow, with parallel sides, feebly sulcate above, not contiguous with the fastigium frontis. *Eyes* rounded, globular. *Pronotum* longer than high and with the insertion on the disc rounded. *Legs :* anterior tibiae armed above, with one or two small spines on the anterior margin ; tympana oval ; posterior femora unarmed beneath ; all the genicular lobes armed with a small spine ; tarsi smooth laterally. *Elytra* with anterior field wide at the base, apex narrow, rounded ; *Sc* and *R* separated ; *Rs* simple ; *M* and *Cu* united at base. *Wings* a little shorter than the elytra. *Subgenital plate* of the male rather long, notched at the apex. *Ovipositor* long, narrow, curved, with margins denticulated along their entire length.

Type species : *Kevaniella bipunctata* sp. n.

This genus is represented by a rather extraordinary insect which is difficult to place systematically. It seems best included among the Pardalotae, although the wings lack an apical triangle.

Kevaniella bipunctata Chopard sp. n. (fig. 12).

Type (♂) and *Allotype* (♀), KENYA, Mandera district: RAHMU, 03° 55′ N., 41° 14′ E., desert-grass and thorn-bush, 19. vi. 1944 (*D. K. Kevan*).

♂, ♀. Size medium, green. *Head* adorned above with a large brown spot which is divided into four parts by three fine, light lines. Fastigium verticis reduced to a narrow projection with parallel margins, feebly sulcate above, separated from the fastigium frontis, the latter a little wider and more strongly projecting. Face smooth, yellow. Antennae slender, the first segment greenish yellow, the others brownish yellow. *Pronotum* greenish with posterior margin blackish brown; two small spots of the same colour situated near the anterior margin; disc rounded in front, flat and slightly elevated posteriorly; anterior margin strongly convex, posterior margin feebly so, almost truncated; lateral lobes longer than high, with the insertion on to the disc rounded; anterior margin of lobe sinuated, inferior margin convex, sub-angulate, with posterior angle rounded and humeral sinus strongly indicated. Prosternum unarmed; meso- and metasterna without lobes. *Legs* long, the femora green, tibiae yellowish; all the femora unarmed beneath but their genicular lobes each provided with a small spine; anterior and median tibiae sulcate above; anterior tibiae unarmed above, armed beneath with six spines on each side, provided with an oval tympanum on either face and rather strongly narrowing after the tympanum; median tibiae shorter than their femora, armed beneath with about ten small spines on each margin. Posterior femora with the filiform apical part comprising half the total length; tibiae very long, armed with about ten small spines in the apical half beneath and about twenty-five (of which two are apical) above. *Elytra* narrow, with internal margin straight, external margin rather convex at the base, parallel to the internal margin from the apical fourth; anterior field wide at base, transparent with rather regular, distant veinlets; posterior field opaque, brownish [purplish in life] with green veins. *Sc* and *R* very slightly separated along their entire length, quite straight; *Rs* emerging after the middle, unbranched; *M* and *Cu* straight, parallel, united at the base and a little before the apex; reticulation close and rather irregular; apices of elytra rounded. Wings extending very little beyond the elytra, transparent except for the apex of the anterior field which is green and brown, particularly in the female; apical triangle absent; *Rs* furcate a little before the apex.

♂. Anterior tibiae without spines. Anal field of both elytra almost similar. Tenth tergite transverse with a feebly concave posterior margin; supra-anal plate square with posterior margin feebly notched, pubescent and with slightly swollen angles; subgenital plate long, narrowing towards the apex and with a narrow angular notch equalling one-quarter of the total length. Cerci strong, curved and flattened, sickle-shaped with acute apices (fig. 12*b*).

♀. Anterior tibiae armed with two small spines on the posterior margin above. Seventh abdominal sternite very large, broader at the apex; subgenital plate rather small, strongly carinated in the middle, having, at the apex, a narrow, short, somewhat rounded notch, the lobes very wide, rounded and somewhat rugose. Ovipositor (fig. 12*c*) long and narrow, of equal width along its entire length, scarcely widening at the base; valves rugose, rather strongly denticulated along their whole margin, the teeth of the superior valve directed towards the apex, those of the inferior valve towards the base.

Measurements: Length of body, ♂, 14 mm., ♀, 18·5 mm.; pronotum, ♂, 3·9 mm., ♀, 4·1 mm.; anterior femur, ♂, 9 mm., ♀, 9·5 mm.; posterior femur, ♂, ♀, 19·5 mm.; posterior tibia, ♂, ♀, 23 mm.; elytra, ♂, ♀, 11·5 mm.; width of elytron, 3·7 mm.; ovipositor, 11 mm.

This rather extraordinary insect differs from the usual run of the Phaneropteridae in the shape of the ovipositor and also in the tarsi which are not sulcate laterally. It seems intermediate in position between the present family and the Meconematidae, but more closely allied to the former.

Distribution: Only known from the type locality.

Fam. Ephippigeridae.

Spalacomimus talpa (Gerstaecker, 1869).

"Guaso Nyiro" (Sjöstedt, 1912). Isiolo : scattered acacia thorn grass land, 3.vi.1946, 1 ♀. Lak Telango : desert-grass and thorn-bush, 26.i.1944, 1 ♂. "Njoro" (Sjöstedt, 1912).

Distribution : East Africa only, but a very common species known from many localities, most of them rather dry.

Madiga aberrans (Schulthess, 1898).

Chopa Gof Crater : Rocky crater rim, on low scrubby bushes, 29.ii.1944. 1 ♂ ; 13.vi.1946, 1 ♂ (nymph) 2 ♀. Dolo (Schulthess, 1898) : one of the type localities. Isiolo : semi-desert-grass and open acacia-thorn, 3.vi.1946, 1 ♀. Marsabit : upland grassland near forest edge, 20.iii.1946, 1 ♀ (nymph).

Distribution : Somalia, Turkana.

Enyaliopis ephippiatus (Gerstaecker, 1869).

Isiolo : semi-desert-grass and open acacia-thorn, 13.vi.1946, 1 ♀. Mt. Kulal : 5900 ft., 9.x.1947, 1 ♀ (*F. W. Bræstrup*) ; *c.* 5700 ft., zone of scattered cedars, 12.x.1947, 2 ♂ (*F. W. Bræstrup*).

Distribution : East Africa, a common species.

Eugaster loricatus Gerstaecker, 1869.

Jaldessa Guda : desert shrub, 3.iii.1944, 2 ♂, 1 ♀ ; 5.iii.1944, 1 ♂, 2 ♀. Mt. Kulal : 3600 ft., in mousetrap, 7.x.1947, 1 ♀ (*F. W. Bræstrup*) ; 5900 ft., 14.x.1947, 1 ♀ (*F. W. Bræstrup*) 4500 ft. zone of scattered cedars, 15.x.1941, 1 ♂ (*F. W. Bræstrup*). Wamba : desert-grass and thorn-bush, 27.ix.1945, 1 ♂.

Distribution : Eastern Africa ; a very common species sometimes of some economic importance.

E. loricatus is said by Jannone (1948) to be sometimes prejudicial to garden and ornamental plants in Eritrea. The same author (1945) mentions that vegetables are damaged and that kitchens of houses may be invaded and household scraps eaten. The Jaldessa Guda specimens were found biting through stored jute sacks in a tent containing maize-meal rations for locust control labour forces operating in this desolate area at the time. Large numbers were attracted to the site and presumably fed upon the meal. The Wamba specimen occurred in the village "street" outside a "shop," suggesting a degree of domesticity.

Eugaster speciosus Sjöstedt, 1912.

This species is possibly only a form of the last.

"Guaso Nyiro" (Sjöstedt, 1912) : Type locality. Lak Telango : desert grass and thorn-bush, 26.i.1944, 1 ♀. Marsabit district (40–50 miles before [i.e., S. of] Marsabit) : x.1947, 1 ♀. (*F. W. Bræstrup*).

Distribution : Only known from the area under discussion.

Fam. Pseudophyllidae.

Zabalius orientalis (Karsch, 1891).

Lugh (Schulthess, 1898): Recorded in the genus *Mataeus* Karsch, 1890.

Distribution: East Africa, Ethiopia. This species is not uncommon in East Africa, where its large size attracts attention.

Cymatomera brancsiki Brunner v. W., 1895.

Since Kirby (1906) synonymized this species with *C. spilophora* Walker, 1870, the name has not been used, but it is doubtful if Kirby's synonymy is correct. Only a complete revision of the genus would decide this point. The specimen agrees fully with the description of *C. brancsiki* but less closely with Walker's and other British Museum specimens of *C. spilophora*. The latter are more robust than the present specimen or others conspecific with it.

Wajir: desert-grass and thorn-bush, vi.1946, 1 ♀ (*J. A. Hunter*).

Distribution: East Africa.

Cymatomera excisa Kevan sp. n. (fig. 13).

Type ♀, Kenya, Mandera district: Damassa, 03° 09′ N., 41° 20′ E., desert-grass and thorn-bush, 19.xii.1944 (*D. K. Kevan*).

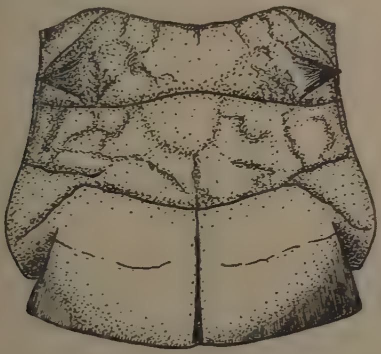
Head: Antennae much longer than the body, set in scrobes immediately in front of the eye; scape twice as long as wide, slightly wider at base than apex, subcylindrical; pedicel twice as long as wide and about half as long and half as wide as the scape, cylindrical; segments of flagellum considerably narrower than pedicel, the two basal segments each about equal in length to it; subsequent segments variable from one and one-half to three times as long as wide; antennal scrobes with raised margins, crescentic, set flat across the front of the head with their inner cornua directed almost vertically upward and almost parallel (the space between them being less than the width of the ridge) and the outer cornua diverging horizontally; ocelli absent; eyes small, almost spherical, their diameter about equal to that of the antennal scape; frons slightly higher than greatest width, one and one-half times as wide at the fronto-clypeal suture as beneath the scrobes, smooth, shiny and without any distinct carinae, grading into the genae; fastigium of vertex, in width, less than the diameter of the eye, produced forwards into a short, acute process (slightly wider at the base than long) between the raised margins of the scrobes. *Pronotum* (fig. 13*a*): Quadrate, somewhat rugose, very slightly shorter than the greatest width, about half as high as wide and with a small, acute, horizontally directed denticle on each side of the prozona; anterior margin arcuately excised; posterior margin rounded, more or less parallel with the anterior margin and descending abruptly at the edges of the disc to form prominent right-angled shoulders with the lateral lobes; lateral lobe about two-thirds as long as the disc; anterior margin of lobe inclined very slightly backward, almost vertical, meeting the lower margin at an obtuse angle; lower margin almost straight, parallel with the dorsum; posterior margin of lobe meeting the lower margin at a rounded right-angle and sweeping round to meet the posterior margin of the disc in a wide arc; median carina of disc obsolete in anterior half, distinct though fine in posterior half; lateral carinae obsolete; typical sulcus placed about the middle of the disc, curved more or less parallel to the posterior margin on the disc but directed backwards on the lateral lobes towards the postero-lateral angle; closely associated with the typical sulcus is an incomplete sulcus which is well developed only on the lateral lobe where it is directed forwards and downwards from a point very close to the lateral angle of the typical sulcus and thus appears to be a branch of it; a second complete sulcus which lies half way between the typical sulcus and the anterior margin of the disc is arcuate in the opposite direction to the margin (i.e., the bend is directed forward in the middle) and continues more or less vertically on to the lateral lobes; on the lateral lobes also, a short distance from the anterior margin, is another incomplete sulcus which runs parallel with the margin for a short distance but does not extend on to the disc; the areas between the sulci are somewhat tumid. *Legs:* Femora flattened, carinate above (particularly the middle femur which is almost flanged) and crenate-dentate below; the femur lengths are in the ratio of 11 : 9 : 18, the middle femur being the shortest; the hind femur slightly exceeds the apex of the abdomen (excluding the ovipositor) and reaches about half as far back as the wings; tibiae flat, rectangular in section; hind tibia equal in length to hind femur. *Tegmina* and *Wings:* Tegmina long oval, about three times as long as wide and with rounded apices, foliaceous and arched over the body, which (combined with the coloration) gives the insect the appearance of a dry stick when at rest, the likeness being enhanced by the presence of about a dozen small, more or less evenly spaced patches of thickened, irregular cross-veinlets within the area bounded by the radius and the cubitus; costal margin strongly rounded, anal margin almost straight in the basal half, costal field very wide, almost one-third of the total width at its widest point (which is at about one-third of the length of the tegmen), basally with coarse, open reticulation in addition to the minute reticulation of the tegmen generally; *Sc* and *R* almost parallel, gently curved, close but separated, anastomosing slightly at the apices; *Rs* emerging just after one quarter of the length of the tegmen, running almost centrally, somewhat undulating; *M* and *Cu* rather sinuous basally but less so for the greatest part of their length, more or less parallel to *Rs* and *R*; all four main veins spaced at very slightly decreasing intervals from *R*. Hind wings wide, a little longer than the tegmina and with the apices less rounded; *Rs* furcate just short of the middle; *M* furcate near the base; cross veins rather regular except at the immediate apex where there is a fine reticulation similar to that of the tegmina. *Abdomen:* Tenth segment very much smaller than the preceding segments and bearing small, curved, tusk-like cerci; epiproct (supra-anal plate) about as wide as long, parallel-sided and rather narrowly rounded at the apex; ovipositor as long as hind femur, very heavily sclerotized, broad, scimitar-shaped, smooth, shiny, unserrated and with bulbously swollen bases to the upper valves and an acute pointed apex which is gradually curved upwards (fig. 13*b*); subgenital plate about two-thirds as long as wide, tapering posteriorly and with a deep triangular notch at the apex.

Coloration: General colour brownish-grey or greyish-white, speckled dark brown or sepia; underside, posterior margin of abdominal terga and palpi ochreous buff; head, pronotum and legs covered with numerous minute sepia brown dots, the frons being unspotted; hind tibiae and some marks on the hind femora suffused reddish chestnut; pleura black; meso- and metasternum, basal part of the first nine abdominal terga, the whole of the tenth and the epiproct pitchy black; ovipositor dark chestnut-brown, margined piceous; tegmina and wings whitish, translucent; longitudinal veins and larger cross veins brownish-buff, the anterior ones (including the radius) yellowish-buff, smaller cross-veins of the tegmina, for the most part, and almost all the cross veins of the hind wings sepia, the wing membrane in the region of the latter being similarly pigmented, giving a tessellated appearance while the thickened patches of veinlets on the tegmina are also heavily pigmented, imparting the stick-like resemblance to the insect at rest.

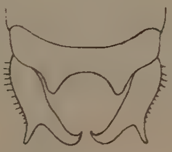
Measurements: Length (excluding wings and ovipositor), 39 mm.; length of head, 4·5 mm.; length of pronotum (middle line), 7 mm.; width of pronotum (maximum), 8 mm.; height of pronotum, 4 mm.; length of tegmen, 47 mm.; width of tegmen, 16 mm.; length of hind femur, 18 mm.; hind tibia, 18 mm.; ovipositor (maximum visible), 18 mm.

This species is very like the last in general appearance and in the reduction in the size and number of pronotal bosses and spines when compared with other species of the genus. It differs from it, and from all other previously described species, in the excised, and not produced, anterior margin of the pronotum. The Ethiopian *Cymatomera hyperborea* Rehn, 1901, has a truncate anterior pronotal margin and a lamellated median pronotal carina; it may be that it should properly be transferred to another genus.

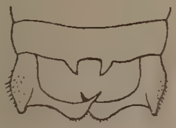
Distribution : The type is unique.



13a



14



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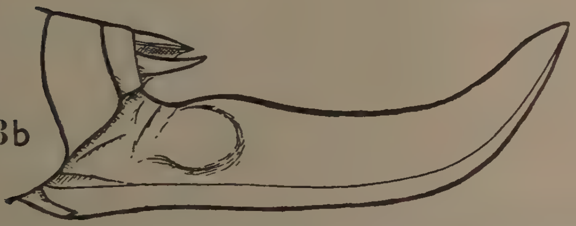

13b

Figs. 13–15.—(13) *Cymatomera excisa* Kevan sp. n. (*a*) Pronotum ; (*b*) ovipositor. (14) *Phlesirtes kevani* Chopard sp. n. Male epiproct and cerci. (15) *Phlesirtes latifrons* Chopard sp. n. Male epiproct and cerci.

Fam. TETTIGONIIDAE.

Phlesirtes bilineatus Chopard sp. n.

Type ♀, KENYA, Marsabit district : CHOPA GOF CRATER, 02° 35′ N., 38° 03′ E., scrub and grass, 13.vi.1946 (*D. K. Kevan*).

Rather large, light testaceous brown with two yellow bands extending from the top of the vertex to the extremity of the abdomen. Fastigium verticis almost twice as wide as the first segment of the antenna, a little rounded at the apex ; superior part a little darkened, possessing, besides the lateral bands, a light median band ; sides strongly diverging as seen from the front. *Face* yellow. *Pronotum* rounded above ; lateral lobes longer than high, strongly narrowing downwards with anterior margin convex, posterior margin straight and inferior margin subangulate ; posterior part with an oval inflation. *Prosternum* armed with two spines. *Abdomen* with parallel margins ; subgenital plate wide with a rounded posterior margin, feebly notched at the apex. Ovipositor long and straight. *Legs :* anterior coxae armed with a spine; the remaining parts of the anterior legs wanting. Median femora short and stout with genicular lobes armed with a spine; tibiae armed beneath with five spines on either side. Posterior femora strongly dilated at base; posterior metatarsi with free plantulae extending almost to the middle. *Elytra* reduced to very small rounded lateral pads.

Measurements: Length of body, 19 mm.; pronotum, 5·5 mm.; posterior femur, 17 mm.; elytra 0·6 mm.; ovipositor, 18 mm.

This differs in its much larger size from any previously known species of the genus.

Distribution: The type is unique.

Phlesirtes kevani Chopard sp. n. (fig. 14).

Type (♂) and *Allotype* (♀) (*in cop.*), KENYA, Mandera district: DAMASSA, 03° 09′ N., 41° 20′ E., desert-grass and thorn-bush, 17.xii.1944 (*D. K. Kevan*).

♂, ♀. Similar to the preceding but much smaller. *Head* adorned with two lateral yellow stripes and a median brown band divided by a fine yellow line. Fastigium verticis wider than the first segment of the antennae; with diverging sides as seen from the front. Face green. *Pronotum* rounded above and with two yellow stripes continuous with those of the head; posterior margin strongly convex; lateral lobes subtriangular, greenish with a rufous band in their superior part. *Abdomen* yellow testaceous above, brown on the sides. *Legs* green spotted with brown. Anterior and median femora rather short and thick, unarmed beneath; genicular lobes armed with a small spine; tibiae, below, with six brown spines on each side. Posterior femora without spines beneath. Posterior metatarsi possessing short, free plantulae. *Prosternum* with two long spines.

♂. Tenth abdominal tergite roundly notched, forming two projecting points, rounded at the apex; subgenital plate wide, feebly notched at the apex, with long styles. Cerci rather short, stout, bearing a feebly curved tooth at about the middle of the external margin (fig. 14). Elytra extending very little beyond the pronotum, reduced to the cubito-anal field only, translucent.

♀. Subgenital plate rather large, rounded, a little truncated at the apex and with a weak median carina. Ovipositor very long, straight. Elytra completely absent.

Measurements: Length of body, ♂, 11·5 mm., ♀, 14·5 mm.; pronotum, ♂, 4·3 mm., ♀, 4·8 mm.; posterior femur, ♂ (lacking), ♀, 15 mm.; elytra, ♂, 1 mm.; ovipositor, 15 mm.

This species is very near to the East African and Ethiopian *Ph. brachiatus* Uvarov, 1923, but the notch of the tenth abdominal tergite is more rounded with less acute angles and the cerci are stouter.

[*Distribution:* Known only from the type locality. There is also a further male (19.xii.1944).—*D. K.*]

Phlesirtes latifrons Chopard sp. n. (fig. 15).

Type ♂, KENYA, N.F.D.: MARSABIT, upland grassland, 26.xii.1944 (*D. K Kevan*).

Same size and appearance as last species but very different in the shape of the vertex and of the cerci. Coloration testaceous with a wide median brown band on the head and pronotum and a similar band on each side extending from the eye to the extremity of the abdomen. *Fastigium* verticis with feebly diverging margins, much wider than the first segment of the antenna, in the form of an equilateral triangle when seen from the front.

Pronotum with metazona a little arched, posterior margin strongly convex, completely covering the elytra ; lateral lobes with feebly sinuated inferior margin and rounded angles, the part near the posterior margin swollen. *Abdomen* a little depressed, with two lateral brown bands enlarged in front ; sides spotted with brown beneath the lateral band ; tenth tergite with a straight margin and a narrow, rather deep apical notch ; angles strongly protruding, narrow, and subacute. Cerci short with basal part thick, ending in a blunt point ; internal tooth very long, slender at the base, ending in a swollen head and having a very acute point (fig. 15). Subgenital plate very large, sulcate in the middle, truncated at the apex and bearing two very short, widely separated styles. *Legs* short, spotted with brown ; anterior and median tibiae armed beneath with five spines on each margin, foramina of the anterior tibiae slit-like. Posterior femora short, thick, unarmed beneath.

Measurements : Length of body, 11 mm. ; pronotum, 5·1 mm. ; anterior femur, 2·8 mm. ; posterior femur, 10·7 mm.

This species is remarkable for the great development of the pronotum, the posterior margin of which covers the elytra completely The shape of the cerci is also characteristic although somewhat recalling *Ph. merumontanum* (Sjöstedt, 1909) from Mt. Meru in northern Tanganyika.

[Additional material is known as follows :

MARSABIT : same data as the type, 3 ♂, 1 ♀. MOYALE : upland grassland, 15.vi.1946, 1 ♂ ; cultivation 8–10.vi.1947, 1 ♀.

The Moyale female agrees with the description of the male (type) in all essentials but is larger (larger also than the ♀ of the last species) and has no elytra. The subgenital plate is rather large, rounded, feebly carinate and slightly truncated at the apex ; the ovipositor is of medium length and slightly curved.

Measurements : Length of body, 13 mm. ; pronotum, 5·1 mm. ; anterior femur, 3·3 mm. ; posterior femur, 12·8 mm. ; ovipositor, 13 mm.

Distribution : Known only from the above localities.—*D. K.*]

Phlesirtes sp. aff. *Ph. brachiatus* Uvarov, 1923.

Very like *Ph. kevani* but a little smaller and with a slightly longer ovipositor.

ISIOLO : 12.i.1937, 2 ♀ (*Dr. B. Benzon*).

Distribution (of *P. brachiatus*) *:* East Africa, Ethiopia.

Phlesirtes sp. ? n.

Similar to the last but smaller and with a much longer ovipositor (14 mm. against hind femur of 10·5 mm.). Possibly new but impossible to describe from a single female.

ISIOLO : 12.i.1937, 1 ♀ (*Dr. B. Benzon*).

Distribution : ?

Clonia kenyana Uvarov, 1942.

CHOPA GOF CRATER : Scrubby bushes on crater rim, 13.vi.1946, 1 ♀ nymph (final instar), presumably this species. MARSABIT (Uvarov, 1942) : type locality.

The record of *Hemiclonia* sp. given by Buxton (1937) doubtless refers to the type of this species for, although he deals mainly with Turkana, he includes also material from the east of Lake Rudolf.

Distribution : Known only from the vicinity of Marsabit.

Fam. CONOCEPHALIDAE.

Conocephalus conocephalus (Linné, 1767).

ALGADA AREA : " Nyika " bush, 4.x.1947, 1 ♀. JALDESSA GUDA : desert-grass, 5.iii.1944, 1 ♀. MOYALE (Ethiopian) (Salfi, 1939).

Distribution : Widely distributed all over Africa ; also known from Italy.

Conocaphalus iris (Serville, 1839).

ALGADA AREA : " Nyika " bush, 4.x.1947, 1 ♀. BURA : desert-grass and thorn-bush (long grass), 16.i.1944, 1 ♂, 1 ♀.

Distribution : Southern and eastern Africa (including Turkana).

Homorocoryphus nitidulus (Scopoli, 1786) ?

BENANE : desert-grass and thorn-bush, 17.v.1945, 2 ♂ (tawny-brown colour form), 1 ♀ (*W. Perera*). BISAN ADI : thorn-bush country, 15.v.1945, 2 ♂ (one tawny) (*W. Perera*). BURA : 28.i.1937, 1 ♀ (tawny) (*Dr. B. Benzon*). GARBA TULA : desert-grass and thorn-bush, 3.vi.1944, 1 ♀. MUDDO GASHI : desert-grass and thorn-bush, 15.vi.1944, 1 ♂ (tawny) 1 ♀. RAHMU : desert-grass and thorn-bush, 19.vi.1944, 1 ♂.

Further Turkana records :

GAPUSS : desert scrub, 4.vi.1945, 1 ♂. LOKITAUNG, iii.1934, 1 ♀ (*D. MacInnes*).

The genus *Homorocoryphus* requires revision. While the specimens cited agree fairly well with European (Italian) examples of *H. nitidulus* it is not at all certain that they do, in fact, all belong to this species.

The Gapuss specimen is rather larger and has the fastigium verticis more raised in profile than in the other examples. The Benane and Bisan Adi specimens (which are very battered) were taken from large, loose swarms occurring in areas of country up to ten square miles in extent (according to the locust scouting officer who collected them). Similar large, loose concentrations are not infrequent in East Africa and the genus is sometimes injurious to crops if present in large numbers. The name *H. vicinus* (Walker) has been used for an injurious swarming form (e.g., by Brédo, 1936 ; Kevan, 1947 ; Mossop, 1951), but that species appears to be distinct (see below). What species is actually involved in the references by these authors is still in doubt. "Phases" analogous to those of certain Acrididae are not unknown among Tettigonioids.

Distribution : H. nitidulus is a very common species, widespread in Southern Europe and, it seems, Africa.

Homorocoryphus vicinus (Walker, 1869) ?

This species was synonymised with the last by Kirby (1906) but reference to Walker's type series shows these to be apparently distinct from European *H. nitidulus*, to some extent in the broader head and less oblique frons and in the larger size (in which features it approaches the next species). It is unlikely that *H. vicinus* merely represents a race of *H. nitidulus* (the genitalia of a male from Walker's series are not very similar to those of that species) but its exact status can only be determined when the genus is revised.

LORIAN SWAMP (Dilmalyali) : On *Echinochloa*, 12.vi.1947, 1 ♀. MARSABIT : upland grassland, 26.ii.1944, 1 ♂, 1 ♀ (both tawny).

It is with hesitation that these specimens are assigned to this species. They are distinct from *H. nitidulus* in the shape of the head, the more truncated anterior and posterior margins of the pronotal disc and in the relative length of the elytra. They approach Walker's series in appearance more than they do the last species but are smaller than the former. The Marsabit examples have very weakly armed hind femora, more in keeping with the next species, but that character is of very doubtful taxonomic value.

Distribution : So far as is known, East and Central Africa. For some references to swarming, see under the last species.

Homorocoryphus longipennis (Redtenbacher, 1891).

This species is very close to the two preceding, differing chiefly in shape of the abdominal extremity and cerci of the male and the longer ovipositor of the female. The armature of the posterior femora used as a distinctive character is very unreliable but the fastigium verticis is wider and the forehead, in profile, less oblique than in *H. nitidulus*.

MOYALE : upland grassland, 15.vi.1946, 1 ♀.

Distribution : Eastern Africa.

Homorocoryphus punctipennis Chopard sp. n.

Type ♂, KENYA, N.F.D. : MARSABIT, upland grassland, 26.ii.1944 (*D. K. Kevan*).

Having the appearance of a small *H. nitidulus*. *Head :* Fastigium verticis a little longer than wide, well rounded at the apex ; head sparsely punctured above. *Face* strongly oblique, green ; mandibles yellow with brown teeth. *Pronotum* rounded in front, flat posteriorly, disc rather coarsely punctured, with a deep furrow at the anterior fourth and a smooth impression a little behind it on the median line ; lateral lobes one and a quarter times as long as high, almost smooth with the inferior margin angulate a little behind the middle, angles rounded ; coloration green with a feeble yellow band on the sides. *Abdomen* green ; tenth tergite widely notched at the apex, with triangular lobes. Cerci stout, armed at the apex with two spines which are directed inwards, the superior spine almost half as long as the inferior one. Subgenital plate wide, carinated in the middle, with a straight posterior margin ; styli rather long, cylindrical. *Legs* green ; anterior tibiae spotted with brown above the tympana ; tarsi brown on the sides. Posterior femora armed with three spines on the infero-internal margin. *Elytra* relatively short, subacute at apex, semitransparent, greenish with green veins and a few small brown spots disposed on a line between the radial and median veins ; a few other small brown spots present in the anal field and at the base of the median vein ; *Rs* emerging a little beyond the middle, unbranched ; anterior field transparent with a close, somewhat irregular reticulation ; *Sc* very thick at the base.

Measurements : Length of body, 21 mm. ; pronotum, 6 mm. ; posterior femur, 25 mm., elytra, 22·5 mm.

Paratypes 2 ♂, same data as type.

These belong to the tawny or greyish-brown condition.

This species is rather similar to *H. nitidulus* in the shape of the abdominal extremity and of the cerci, but it is remarkable for the short elytra spotted with brown.

[*Distribution :* Known only from Marsabit, it may be a local subspecies which has evolved in this isolated locality.—*D. K.*]

3. Superfam. GRYLLOIDEA.

Fam. Gryllotalpidae.

Gryllotalpa africana Palissot d. B., 1804.

Bura : Tana River bush (at light), 16.i.1944, 1 ♂. " Guaso Nyiro " (Sjöstedt, 1912). Mt. Nyiro (Bolívar, 1922) : Recorded in the genus *Curtilla* Oken, 1815. Pangali : v.1943, 1 ♂ (*E. Opiko*). Tana River (unknown locality) : vi.1937, 2 ♀ (*R. E. Toker*).

Distribution : Africa (including N. Turkana)[8], Spain, Canaries, Tropical Asia, Japan, Australasia.

Fam. Gryllidae.

Brachytrypes membranaceus (Drury, 1773).

Moyale : Cultivation : 8–10. vi. 1947, 1 ♂ (found dead). Wamba : desert-grass and thorn-bush (under débris), 31.iii.1946, 1 ♂.

Distribution : East, Central and West Africa.

Gryllus maurus (Afzel and Brann, 1804), **comb. nov.**[9]

Acheta morio Fabricius, 1781, *Spec. Ins.* **1** : 354.
Acheta maurus Afzel and Brann, 1804, *Achet. Guin.* : 22, no. 3, fig. 4.

Isiolo : scattered acacia-tree grassland (under débris), 3.vi.1946, 1 ♀. Moyale (Ethiopian) (Salfi, 1939) : recorded as *G. morio*.

Distribution : East, Central and West Africa.

Gryllus bimaculatus Degeer, 1773.

Algada area : " Nyika " bush, 4.x.1947, 1 ♀. Bambota : desert-shrub, 6.vi.1946, 1 ♂. Bardera (Giglio-Tos, 1917) : recorded in the genus *Acheta*. Bulessa Kulal : 5.x.1947, 1 ♀ (*F. W. Bræstrup*). Between Bulessa Kulal and Kulal : 3900 ft., 12.x.1947, 1 ♀ (*F. W. Bræstrup*). Mt. Kulal : x.1947, 1 nymph (*J. G. Williams*) ; 6.x.1947, 1 ♂, 3 ♀ (*F. W. Bræstrup*). Kulal (south of): viii.1944, 1 ♂ (*J. Adamson*). Nr. MUDDO GASHI: desert-grass and thorn-bush, 2.i.1947, 1 ♂, 1 ♀ (*M. H. Wraith*). LAK BOGGAL: desert-grass and thorn-bush, v.1947, 1 ♂ (*G. MacIntosh*). LAK TELANGO: desert-grass and thorn-bush, 26.i.1944, 1 ♀. LAKE RUDOLF (probably near EL MOLO): ix.1944, 1 ♀ (*J. Adamson*). MT. MARSABIT: upland grassland near forest, 9.x.1944, 1 ♀. MOYALE (Ethiopian) (Salfi, 1939). SABENHA: dust and desert-grass, 12.vi.1947, 1 ♂, 2 ♀. SAMBURU district: vi.1944, 1 ♀ (*E. Opiko*). TULA No. I: x.1940, 2 ♀ (*A. R. Melville*).

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[8] Chopard (1938) records it from " Ethiopie : Namoropus," i.e., Namoruputh, which now lies within the Turkana administrative area, cf. Kevan (1950*a*).

[9] Since Fabricius' *Acheta morio* was not transferred to the genus *Gryllus* until 1791 (Olivier, *Encycl. Méth. Ins.* **6** : 636), the combination *Gryllus morio* becomes a secondary homonym of *Gryllus morio* Fabricius, 1787, *Mant. Ins. Hafn.* **1** : 238 (**hom. nov.**)—which is itself a synonym of *Gryllus fuscus* Pallas, 1773 (cf. Ander, 1952)—and cannot now stand. The first valid name available appears to be *Acheta maurus* Afzel and Brann.—D. K.

Buxton (1937) in recording the species from Turkana gives no exact locality; his specimens (2 ♂, 2 ♀) are from Fergusson's Gulf, Lake Rudolf, May-June, 1934 (*D. R. Buxton*).

Distribution: One of the commonest crickets in East Africa; of wide distribution embracing southern Europe, almost all Africa and parts of Western Asia.

Acheta domesticus (Linné, 1758)

BARDERA (Giglio-Tos, 1917): Recorded as *Gryllus*. JANJU: desert-grass and thorn-bush, 24.i.1944, 1 ♂. LUGH (Giglio-Tos, 1917). MANDERA: desert-grass and thorn-bush (in house), 22.x.1944, 1 ♂. MANSUR (Giglio-Tos, 1917). SERENLI: desert-grass and thorn-bush, 21.x.1946, 1 ♂.

There is also an additional badly damaged specimen, probably of this species from MARSABIT (under small bridge, 3.x.1947, *F. W. Bræstrup*).

Further Turkana record:

LORUGUMU: 6.vi.1945, 1 ♂.

The specimens differ somewhat from examples living in houses in Europe although they certainly belong to the same species. They presumably belong to "var." *meridionalis* Uvarov, 1921. The Lorugumu example is very large and the Janju and Mandera specimens have the head brownish above with a very faint yellow frontal band.

Distribution: Cosmopolitan, but apparently endemic to these dry parts of Africa. Like earlier Turkana records (Buxton, 1937)[10], the above specimens, except for the Mandera example (and Giglio-Tos' material ?), were all captured in the open at considerable distances from any human habitation. It is interesting to note the beginnings of a domestic association shown by the Mandera specimen.

Acheta xanthoneurus (Gerstaecker, 1869).

ALESSANDRA: 1931 (?), 1 ♂, 1 ♀ (in Municipal Museum, Mogadishu, Somalia).

BURA: Tana River bush (under débris), 16.i.1944, 1 ♂, 1 ♀.
Distribution: East Africa.

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[10] Data not previously given; specimens in British and Coryndon Museums bear similar labels to Buxton's specimens of *Gryllus bimaculatus* (above).

Acheta palmetorum (Krauss, 1902).

Algada area : "Nyika" bush, 4.x.1947, 1 ♂, 1 ♀. Rahmu : desert-grass and thorn-bush, 19.vi.1944, 1 ♂.

Turkana record :

Fergusson's Gulf : May–June, 1934, 1 ♀ (*D. Buxton*).

Distribution : This species was formerly known only from the oases of North Africa ; it seems to be much more widespread than was to be expected. In addition to North Kenya it also occurs in Somalia ; it was previously wrongly recorded from Turkana as *Gryllus conspersus* (Saussure, 1869) by Kevan (1950*a*).

Acheta beibienkoi (Chopard, 1938).

Birchika . desert-grass and thorn-bush, 7.xii.1944, 1 ♀ ; 8.xii.1944, 1 ♂.

Distribution : Described from south-west Ethiopia and found also in East Africa including N. Turkana (Namoruputh, see footnote 8, p. 342).

Acheta laticeps (Chopard, 1939) (fig. 16).

Algada area : "Nyika" bush (on Black Cotton soil), 4.x.1947, 1 ♂.

Distribution : Described from Central Africa (Congo) and known also from East Africa.

Acheta zolotarewskyi Chopard sp. n. (fig. 17).

Type ♂, Batha, Ati[11], 14.xi.1933 (*B. N. Zolotarewsky*), [Paris Museum].

Rather close to *A. laticeps* but larger. *Head* wider than the pronotum in front, rufous brown above with scarcely visible yellow lines on the occiput; frontal rostrum twice as wide as the first antennal segment. Face short and wide, brown, shining ; facial shield convex ; clypeo-frontal suture subtriangular, extending to the middle of the antennal scrobes. Lateral ocelli wide apart on account of the width of the frontal rostrum ; anterior ocellus very strongly and transversely elongated. *Pronotum* somewhat widening anteriorly, blackish brown with a few rufous markings ; lateral lobes blackish with yellow anterior angles. *Genitalia* (fig. 17) of the same type as *A. laticeps* (fig. 16) but with the angles of the bridge produced in a long, narrow plate which is curved and acute at the apex. *Legs* brownish ; posterior tibiae armed with six internal and seven external spines. *Elytra* scarcely extending to the apex of the abdomen, translucent with brown veins and brown spots in the anal field and between the chords ; mirror almost regularly square with a feeble dividing vein placed behind the middle ; diagonal vein and chords long ; two oblique veins ; apical field short with three sectors and a few large cells only ; lateral field blackish with close veins ; *Sc* giving off three branches. *Wings* very short.

Measurements : Length of body, 14·5 mm. ; pronotum, 2·6 mm. ; posterior femur, 8 mm. ; elytra 8·5 mm.

Allotype ♀, Kenya, N.F.D. : Isiolo, under débris, 3.vi.1946 (*D. K. Kevan*).

Head and *legs* as in the male ; head with a very narrow yellow line between the ocelli. *Pronotum* very feebly enlarged in front with partly yellowish lateral lobes. *Elytra* extending to the apex of the fourth abdominal tergite, dorsal field with eight regular, feebly oblique veins, four of which are branches of the cubital vein ; transverse veinlets close and regular ; lateral field with close veins, *Sc* giving off two branches.

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[11] This locality presumably refers to a point on the Wadi Batha in the proximity of Ati or Aty, 13° 14′ N., 18° 18′ E., in French Chad.—D. K.

Measurements : Length of body, 17 mm. ; pronotum, 3·1 mm. ; elytra, 7 mm. ; ovipositor, 11·5 mm.

This species is very close to *A. laticeps*, having the wide head, short face and the clypeo-frontal suture rather strongly angulate and extending a little above the inferior margin of the antennal scrobes. The male genitalia are also of the same type as *A. laticeps* but still closer to *A. guanchicus* (Krauss, 1892) (from the Canary Islands), with which species it also has evident affinities. Although the locality of the allotype female is rather different from that of the male type, it seems quite certain that both belong to the same species.

There is also a second female, KENYA, Isiolo district : JANJU, 01° 40′ N., 39° 05′ E., desert-grass and thorn-bush, 24.i.1944 (*D. K. Kevan*). This probably represents the macropterous condition of the species ; the elytra extend to the apex of the abdomen and the subcostal vein gives off four branches. The wings are caudate.

Acheta melanocephalus (Serville, 1839)?

DOLO (Schulthess, 1898) : identification doubtful (as *Gryllus*).
Distribution : India.

Gryllodes sigillatus (Walker, 1869).

MARSABIT : in hut, 25.iii.1944, 1 nymph (♂). WAJIR : in house, 4.i.1945, 2 ♂, 2 ♀ ; 2.ii.1947, 2 nymphs (*M. H. Wraith*).

Distribution : This widely distributed cosmotropical species is common in Africa south of the Sahara, especially in houses.

Gryllopsis physomerus (Gerstaecker, 1869) (figs. 18*a* and *b*).

" GUASO NYIRO " (Sjöstedt, 1912) : as *Gryllodes*.
Distribution : East Africa, including Turkana.

Gryllopsis scenicus (Gerstaecker, 1869).

" MONT KAROLI " (Bolívar, 1922).
Distribution : East Africa.

Gryllopsis latipennis Chopard sp. n. (fig. 19).

Type ♂, KENYA, N.F.D. : ISIOLO, in old hut, 3.vi.1946 (*D. K. Kevan*).
Paratype ♂, KENYA, N.F.D.: south of KULAL, viii.1944 (*J. Adamson*).
A species very close to *G. amplipennis* Chopard, 1928, from Uganda, but smaller, with elytra less strongly enlarged posteriorly.

Head above with a rather wide yellow band extending from one cheek to the other. Face yellow, more strongly swollen than in *G. amplipennis*, adorned between the antennae with an angular brown band. *Elytra* brown with yellowish veins ; mirror strongly transverse (but not so much so as in *G. amplipennis*) with a regularly convex internal margin ; diagonal vein short and almost straight (not strongly sinuated as in *G. amplipennis*) ; four almost horizontal, parallel chords, the two last of which are united at the base ; apical field short, with four sectors and the reticulation less close than in *G. amplipennis*. *Posterior tibiae* armed with five spines on each margin. *Genitalia* (fig. 19) of the same type as *G. amplipennis* (figs. 20*a*, *b*) and *G. physomerus* (figs. 18*a*, *b*), differing from both in the median piece (which seems to play the part of the spermatophore sac of other Gryllids) being plain instead of denticulated.

Measurements : Length of body, 17·5 mm. ; pronotum, 4·1 mm. ; posterior femur, 12·5 mm. ; elytra, 11 mm.

Distribution : Known only from the localities given.

Gryllopsis unicolor Chopard sp. n. (fig. 21).

Type ♂, Kenya, N.F.D. : Wajir, at light (in house), 17.x.1944 (*D. K. Kevan*). Another species of the *physomerus*-group but with a much more uniform coloration.

Head large, globular, rufous yellow above with an arched dark band between the antennae ; frontal rostrum very wide, rounded. Face yellow, strongly swollen, finely grooved. Antennae and palpi yellow ; fifth segment of maxillary palpi longer than the fourth, feebly enlarged at the apex (much longer than in *G. physomerus*). *Pronotum* a little narrowing in front, with straight anterior and posterior margins ; disc convex ; lateral lobes light yellow, with inferior margin ascending posteriorly and with rounded angles. *Abdomen* light brown above, yellow beneath ; tenth tergite and supra-anal plate yellow ; subgenital plate large, boat-shaped. Cerci yellow. *Genitalia* (figs. 21*a*, *b*) short, strongly curved, median piece laterally denticulated, rounded at the top. *Legs* yellowish, pubescent. Anterior tibiae with a large, oval external tympanum, armed at the apex with two long inferor spurs ; metatarsi and second tarsal segments spinulose beneath. Median tibiae dilated in the middle. Posterior femora stout, yellowish with a brown pubescence, very faintly darkened at the apex ; tibiae armed with six spines on either margin, the first very small ; inferior apical spurs rather long, the external a little longer than the internal one ; medio-external spur extending to the middle of the metatarsus, supero-external spur a little shorter ; the two large internal spurs, particularly the superior one, very long ; metatarsus long, a little compressed, armed with four small spines on each margin and two apical spurs. *Elytra* extending to the apex of the abdomen, greyish with yellow veins ; anal field very short ; mirror a little wider than long, angulate in front, rounded posteriorly, divided in the middle by a feebly curved vein ; diagonal vein short, almost straight ; first and second chords curved, parallel, the first one united with the mirror by a small vein ending near the anterior angle ; oblique veins four in number ; apical field rounded, with three sectors and a rather close, somewhat irregular reticulation ; lateral field very high ; *Sc* giving off three branches. *Wings* abortive.

Measurements : Length of body, 17 mm. ; pronotum, 4 mm. ; posterior femur, 12 mm. ; elytra, 9·5 mm.

This species is close to *G. physomerus* but it possesses a more uniform coloration, the posterior femora being scarcely darkened at the apex and without a light pre-apical ring ; the pronotum is feebly narrowed in front ; the elytral venation is almost similar to that of *G. physomerus* but the genitalia are much shorter.

Distribution : Known only from Wajir.

Scapsipedus marginatus (Afzel and Brann, 1804).

ALGADA AREA : "Nyika" bush, 4.x.1947, 2 ♀. BALAMBALA : ix.1947. 1 ♂ (*J. Adamson*). BIRCHIKA : desert-grass and thorn-bush, 9.xii.1944, 1 ♀, BURA : Tana River bush (under débris), 16.i.1944, 1 ♂, 1 ♀. HABASWEIN (5 miles N.E.) : desert-grass and thorn-bush, 2.iii.1945, 1 ♀. MT. KULAL : 2600 ft., 16.x.1947, 1 nymph (*F. W. Bræstrup*) ? this species. MANDERA : in house, 22.x.1944, 1 ♀. RAHOLE : thorn-bush (under potsherd), 6.i.1944, 1 ♂, 1 ♀.

Distribution : This species is very common and widely distributed all over tropical Africa (including Turkana).

Scapsipedus limbatus Saussure, 1877.

This species may be merely a form of the last.

ALGADA AREA : "Nyika" Bush (black Cotton soil), 4.x.1947, 2 ♂.

Distribution : Described from Madagascar.

Scapsipedus nigriceps Chopard sp. n.

Type ♂, KENYA, N.F.D., ISIOLO : iii.1944 (*Mrs. J. Adamson*).

General aspect of a small *Gryllus bimaculatus*. *Head* large, completely black ; frontal rostrum very wide ; face very wide ; very strongly flattened, even feebly concave ; clypeo-frontal suture arched, post-clypeus very narrow. Mandibles reddish. Palpi brown ; cheeks feebly wrinkled. *Pronotum* scarcely widening in front, with a concave anterior margin and a straight posterior one ; disc feebly convex, furrowed in the middle, somewhat tinged with rufous brown ; lateral lobes black, with a straight inferior margin. *Abdomen* and cerci black. *Genitalia* of a very simple shape, trilobate with the median lobe large and triangular. *Legs* black, short, pubescent. Anterior tibiae no longer than the femora, with large oval external tympana and small rounded internal ones ; two external apical spurs, the inferior one long, one internal inferior spur even stouter than this ; tarsi as long as the tibiae, the metatarsus longer than the other tarsal segments together, stout, armed beneath with two rows of spinelets. Median legs similar to the anterior ones, with slightly longer tibiae and tarsi. Posterior femora very stout ; tibiae armed with eight strong and close external spines and six still stronger internal ones ; apical spurs very strong, the two large internal ones exceeding half the length of the metatarsus ; this last armed with seven or eight denticles on each margin. *Elytra* as long as the abdomen, shining black with a yellow humeral spot and another on the anal knot ; mirror almost as wide as long, with almost rounded anterior and internal angles ; dividing vein a little beyond the middle, curved ; diagonal vein rather short, straight ; chords rather strongly curved ; four oblique veins ; apical field rather long, rounded, with six sectors and a rather regular, square reticulation ; lateral field black, with five regularly spaced veins. *Wings* short.

Measurements : Length of body, 11·5 mm. ; pronotum, 4 mm. ; posterior femur, 12·2 mm. ; elytra, 12 mm.

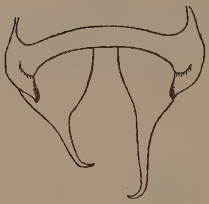
This species looks very like *S. luctuosus* I. Bolívar, 1910, from West Africa, but the genitalia of the latter are deeply divided into three long, narrow lobes, the median of which is curved upwards ; in *S. lesnei* Chopard, 1935, from Mozambique, which is also very closely related, the three lobes are almost equal.

Distribution : Known only from the type locality.

Pteronemobius dumosus (Karsch, 1893).

Mt. Marsabit : By forest stream, 21.xi.1944, 1 ♂.

Distribution : Tropical Africa.



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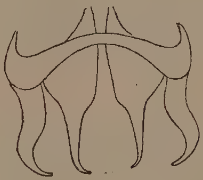

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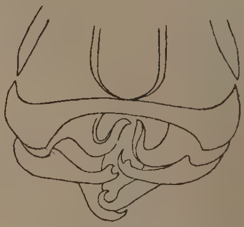

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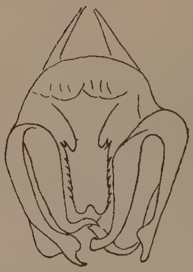
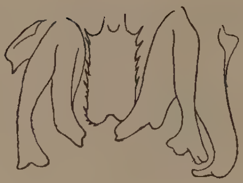
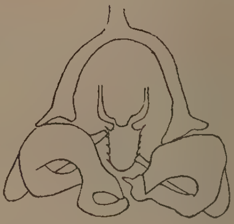


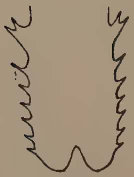
18a



20a



21a



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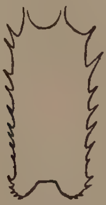
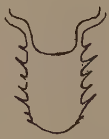


20b



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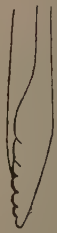

22

Figs. 16–21.—Male genitalia of : (16) *Acheta laticeps* (Chopard). (17) *Acheta zolotarewskyi* Chopard sp. n. (18) *Gryllopsis physomerus* (Gerstaecker), (*a*) entire ; (*b*) median piece. (19) *Gryllopsis latipennis* Chopard sp. n. (20) *Gryllopsis amplipennis* Chopard (type), (*a*) entire ; (*b*) median piece. (21) *Gryllopsis unicolor* Chopard sp. n., (*a*) entire ; (*b*) median piece.

Fig. 22.—*Arachnocephalus kevani* Chopard sp. n., apex of ovipositor.

Pteronemobius aethiops (Saussure, 1877).

Lugh (Giglio-Tos, 1917): Recorded in the genus *Nemobius* Audinet-Serville, 1839.

Distribution: Tropical Africa.

Fam. Mogoplistidae.

Arachnocephalus kevani Chopard sp. n. (fig. 22).

Type ♀, Kenya, Mandera district: Damassa, 03° 09′ N., 41° 30′ E., desert-grass and thorn-bush, 19. xii. 1944 (*D. K. Kevan*).

Paratypes 2 ♀: Same data as type.

Size medium for the genus; *head* and *thorax* rufous brown, *abdomen* blackish; during life the body must have been covered with grey and white scales[12] which are still in the dried condition rather abundant on the sides and on the posterior legs. *Head* a little flattened; frontal rostrum almost one and a half times as wide as the first antennal segment, rounded at the tip, furrowed in the middle. Face blackish brown except for the clypeus, which is yellow. Palpi rufous; the three last segments of the maxillary palpi rather long, almost equal, the fifth feebly enlarged and darkened at the apex. *Pronotum* as wide as long, with straight anterior and posterior margins. Anterior and median *legs* relatively long, bearing a few white bristles, the femora strongly darkened. Posterior femora covered with whitish scales. *Ovipositor* long and straight; apical valves very feebly wider than the stem, the superior ones bearing five rounded teeth on their inferior margins (fig. 22).

Measurements: Length of body, 8·2 mm.; pronotum. 1·7 mm.; posterior femur, 5 mm.; ovipositor, 7 mm.

This species is very close to *A. meruensis* (Sjöstedt, 1909), but is a little larger with a wider frontal rostrum and longer maxillary palpi and legs.

[Besides the type and paratypes there is another specimen of the same species as follows:

Chopa Gof Crater: Among low shrubs, 29. ii. 1944, 1 ♀.

Distribution: Known only from the localities mentioned.—*D. K.*]

Fam. Trigonidiidae.

Anaxipha longipennis (Serville, 1839)?

Sálagle (Giglio-Tos, 1917): Identification doubtful; recorded in the genus *Cyrtoxiphus* Saussure, 1878.

Distribution: The species was described from Mauritius.

Fam. Phalangopsidae.

Homoeogryllus reticulatus (Fabricius, 1781).

Alessandra: 1931 ?, 2 ♂ (in Municipal Museum, Mogadishu, Somália).

Distribution: Eastern Africa.

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[12] It was—D. K.

Guasacris variegata Sjöstedt, 1912.

"GUASO NYIRO" (Sjöstedt, 1912): type locality.
Distribution: Known only from the type locality.

Gryllomimus chopardi (Ebner, 1935).

JALDESSA GUDA: desert-grass, 5.iii.1944, 1 ♀.

Distribution: This interesting small species was previously known only from the Anglo-Egyptian Sudan and from Turkana.

Fam. ENEOPTERIDAE.

Euscyrtus sp.

Specimens of this species are not now available for study, but a notebook entry by the junior author suggests that they may be close to *E. bivittatus* Guérin-Méneville, 1844.

ALGADA AREA: "Nyika" bush, Black Cotton soil (among *Sporobolus* sp.), 4.x.1947, 1 ♂, 1 ♀.

Distribution: ?

Dolichogryllus griseus Chopard, 1934.

BIRCHIKA: desert-grass and thorn-bush, 20.vi.1944, 1 ♂; 7.xii.1944, 1 ♂. DAMASSA: desert-grass and thorn-bush, 17.xii.1944, 1 ♂. FINNO: desert-grass and thorn-bush, 17.v.1944, 1 ♂. HABASWEIN (5 miles N.E.): desert-grass and thorn-bush, 22.i.1944, 1 ♂. JANJU: desert-grass and thorn-bush, 24.i.1944, 1 ♂. MUDDO GASHI: desert-grass and thorn-bush, 8.vi.1944, 1 ♂. RAHMU: desert grass and thorn-bush, 19.vi.1944, 1 ♂. SAMBURU district: vi.1944, 1 ♀ (*E. Opiko*). WONTE GODA: desert-grass and thorn-bush, 14.xii.1944, 1 ♂; 16.xii.1944, 1 ♂.

The female was previously unknown. The following is a description of the Samburu example:

Shape and general aspect as in the male, but a little larger and stouter; brown markings weak on the head and legs; posterior femora wholly yellowish, tibiae spotted with brown only at the base of the spines. *Abdomen* yellowish brown; subgenital plate rather large, very widely notched at the apex, the notch being deep and angular, the lobes being at right angles; ninth tergite with posterior margin feebly notched in the middle and bearing a small projection; tenth tergite with prominent yellow margins; supra-anal plate truncated at apex. Ovipositor rather short and stout; apical valves oval, finely shagreened and bearing at the apex, two oblique teeth. *Elytra* testaceous brown with a dark band on the superior part of the lateral field; dorsal field with very confused venation, the principal veins almost lost in the reticulation which is formed of large irregular, lengthened cells, but six sectors of the cubital vein may be distinguished; lateral field with an oblique, regularly spaced vein; *Sc* giving off eight branches. *Wings* a little longer than the elytra.

Measurements: Length of body, 19 mm.; pronotum, 3 mm.; posterior femur, 11 mm.; elytra, 15 mm.; ovipositor, 10 mm.

Distribution: This species was described from Bura in Kenya—not from the locality of this name on the R. Tana in the area under review, but presumably the low dry country near Bura, S.E. Kenya, whence the species has also been recorded by Kevan (1950). It was discovered again in the Turkana Desert (Chopard, 1938) and is one of the commonest crickets in the arid region which extends from Turkana to British Somaliland ; only the one female has ever been observed.

III. DETAILS OF COLLECTING STATIONS NOT PREVIOUSLY LISTED.*

Station.	Political district.	Latitude.	Longitude (East).	Approximate altitude.	Topography.
Alessandra (Towata I.)	Kismayu (Somalia)	00° 30′ N.	42° 46′	?75′	Flat island in river.
Bambota	Isiolo	01° 20′ N.	38° 20′	1150′	Flat, sandy.
Benane	Isiolo	00° 29′ N.	38° 38′	1500′	Rather eroded, sandy.
Bisan Adi	Isiolo	00° 05′ N.	38° 20′	1800′	Flat, eroded, rocky.
Bulessa Kulal	Marsabit	02° 30′ N.	37° 03′	1600′	Flat, sandy, rather eroded.
El Molo (Elmolo)	Marsabit	02° 50′ N.	36° 42′	1250′	Bare lava ridges by lake shore
Fergusson's Gulf	C. Turkana	02° 30′ N.	37° 57′	1250′	Sandy spit.
Hagadera	Garissa	00° 02′ N.	40° 25′	467′	Flat, sandy.
Lak Boggal	Wajir	01° 17′ N.	39° 53′	700′	Flat, sandy.
Lorian Swamp (Dilmalyali)	Wajir	00° 53′ N.	39° 33′	600′	Grey mud and swamp.
Mansur (east bank of R. Juba)	Bardera (Somalia)	02° 12′ N.	42° 14′	335′	Flat, black soil.
Mt. Nyiro	Samburu	02° 08′ N.	30° 47′	? (summit 9203′)	Steep mountain slope.
Sabenha	Wajir	00° 54′ N.	39° 30′	600′	Plains, grey soil.
Serenli	Bardera (Somalia)	00° 22′ N.	42° 18′	400′	Rather eroded, red soil.
Tula No. I	Garissa	00° 35′ S.	39° 17′	750′	Rather eroded, sand and clay.

* Details of the majority of the collecting stations have already been given (see Kevan and Chopard, 1954 ; Kevan, 1954 ; Chopard and Kevan, 1954.)

IV. SUMMARY.

This study of Ensifera from certain dry parts of eastern Africa follows those dealing with other orthopteroid groups (*see* Kevan and Chopard, 1954 ; Kevan, 1954, 1954*a*, 1954*b* ; Chopard and Kevan, 1954). A list of species together with some observations is given. A considerable proportion (nearly one-third) of the species are described as new.

Four species of Gryllacridoidea are recorded, of which *Stictogryllacris pallidus* is new. No less than 55 species of Tettigonioidea (of which 36 are Phaneropterinae) are known from the area under consideration, and of these a score are new, as follows : *Peronura viridis*, *P. vicina*, *P. diminuta*, *P. samburu*, *Tropidonotacris carinatus*, *Phaneroptera acaciae*, *Melidia laminata*, *M. kenyensis*, *Terpnistria tuberculata*, *Diogena denticulata*, *Tylopsis gracilis*, *Eurycorypha kevani*, *E. simillima*, *Plangiodes carinatus*, *Kevaniella bipunctata*, *Cymatomera*

excisa, *Phlesirtes bilineatus*, *Ph. kevani*, *Ph. latifrons* and *Homorocoryphus punctipennis*. The genera *Tropidonotacris*, *Plangiodes* and *Kevaniella* are also new. *Horatosphaga trochlearis* Bol. has been transferred to the genus *Peronura*. Of the 28 Grylloidea listed, 5 are new, namely : *Acheta zolotarewskyi*, *Gryllopsis latipennis*, *G. unicolor*, *Scapsipedus nigriceps* and *Arachnocephalus kevani*. It is also noticed that the well-known name *Gryllus morio* (F.) must fall in favour of *G. maurus* (Afz. & Brann). The unknown female of *Dolichogryllus griseus* Chopard is also described.

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Vol. 105. Part 15. Pp. 355–372. 22 figs. 15th November, 1954

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PUBLISHED BY THE SOCIETY AND
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THE ADULT STAGES OF *PROSOPISTOMA* LATREILLE (EPHEMEROPTERA), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM AFRICA.

By M. T. Gillies, M.B., F.R.E.S.

Manuscript received 3rd March, 1954.

(Read 5th May, 1954.)

With 22 Text-figures.

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1. Introduction and Acknowledgments.

Nearly two centuries have elapsed since Geoffroy (1762) described and figured an insect, found in streams near Paris, as *Binoculus haemisphericus, cauda foliacea, capitis puncto triplici fusco*, "le binocle à queue en plumet". His figures, exact in all important details excepting only the number of caudal appendages, constitute the first remote but recognisable description of this unique aquatic insect. Fourcroy (1785), in listing and applying the binomial system to Geoffroy's species, designated it as *Binoculus foliaceus*. Latreille (1833) separated *foliaceus* from the other Crustacea with which it had previously been aligned, but still regarded it as a branchiopod and created the genus *Prosopistoma* to include both *foliaceum* (as *punctifrons*) and a newly discovered species from Madagascar. Little was seen of *foliaceum* throughout the century that followed Geoffroy's description. In 1868 it was re-discovered by E. Joly, a military surgeon in the French Army who, it is related, found time to collect insects in many rivers of France before and during "the disastrous war" of 1870–71. Joly (1871) and Joly and Joly (1872) were the first to recognise the true nature of Geoffroy's "binocle" as the immature stage of an insect, and correctly assigned it to the Ephemeridae.

The adult remained unknown. In the years that followed, the suggestion was made that reproduction was accomplished in the aquatic phase, and Vayssière (1881*a*, *b*) recounted how this prompted him to study the living insect in the laboratory and how this led to the breeding out of the two unique female subimagoes in the early summer of 1880. It seems that Vayssière's confidence in announcing the discovery of "l'état parfait" was not fully shared by his contemporaries. Eaton (1884), in his section on *Prosopistoma*, remarked

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rather primly that " in accordance with my usual custom, I refrain from passing criticisms upon the work of previous authors", and most subsequent writers have concluded that the real adult, the imago, had not been obtained.

From that date onwards, despite the relative abundance of *foliaceum* in certain rivers of France and its discovery in Sweden, Germany and Czechoslovakia, and despite the finding of other species in Africa and the East Indian Archipelago, no imagoes have been seen. Only after another 45 years could Vayssière (1925) again report the capture of an ill-preserved female trapped in the shuck of a mature nymph bred in his laboratory. The nymph of *Prosopistoma* is set apart from all other Ephemeroptera expect *Baetisca* by the limpet-like development of the mesonotum in the form of a carapace, and it differs from this latter insect in several important respects. It has been described in detail by Vayssière (1882, 1890*a*), Eaton (1884), Lestage (1921) and Lieftinck (1932) and discussed by many other authors, among them Trägårdh (1911), Alm (1918) and Lestage (1925). The female subimago also, even though figured by Vayssière " under very disadvantageous circumstances", as Eaton put it, was shown to differ strikingly from all other Ephemeroptera, and this, coupled with the continued elusiveness of the imago and the male, has helped to create an aura almost of mystery around it.

At the present time, some five or six closely allied species of *Prosopistoma* have been recognised in the nymphal state, distributed as follows :

P. foliaceum (Fourcroy), 1785, Continental Europe.
P. variegatum Latreille, 1833, Madagascar.
P. de guernei Vayssière, 1893, Senegal.
P. species Vayssière, 1936 (as *de guernei*), Kenya.
P. species Paulian, 1947, Belgian Congo.
P. wouterae Lieftinck, 1932, Java ; Sumatra (Ulmer, 1939).

Elsewhere in Africa, nymphs are found in the Kenya Highlands " in nearly all rivers flowing eastwards from Mount Kenya and the Aberdares, at altitudes between 5000 and 6500 feet " (information kindly supplied by Dr. V. D. Van Someren), and in Natal in South Africa (R. S. Crass, *in litt.*). In 1951, nymphs were found by the present writer in the Sigi River in the Eastern Usambara Mountains of Tanganyika. In subsequent years, after attempted rearing in the laboratory had failed, adults of both sexes were bred out in a concrete tank constructed by the riverside, and the evidence this afforded of the emergence season of the adults led to the capture of many others on the wing in nature.

The material obtained in this way forms the basis of the long delayed description of the adult stages of *Prosopistoma* given here. It is hoped that this account may answer some of the questions raised by earlier writers, whose speculations during the three-quarters of a century following Vayssière's discovery have added much to the interest and pleasure of the present studies. In addition, Mr. R. S. Crass has generously asked me to describe the South African nymph discovered by him. He has already bred out a female of this species, and it is to be hoped that further adult material will be obtained in the future.

Reference should be made to the selection of the type species of *Prosopistoma*. Latreille did not indicate which of the two species he considered as representative of the genus; but it could well be argued either that *variegatum* should be the type as being the insect he had before him at the time, or that *foliaceum* should be chosen on the grounds that Latreille referred to Geoffroy's species as " le prototype de mon crustacé", as well as being the better known and more readily available of the two. Eaton (1884) was the first author to designate a type, and chose *variegatum*. Eaton therefore was free to select either species, and by application of Article 30 of the International Rules this subsequent designation of *variegatum* is not subject to change. Lieftinck's objection that *variegatum* is an undescribed species and therefore invalidated as a type cannot be upheld. This conclusion was apparently based on the specific diagnosis given by Eaton (1884) and ignores the fact that Latreille described it as different from *foliaceum* in terms that, at the time, seemed adequate to him. In addition, Westwood (1877) gave figures of *variegatum* that show the characteristic short antennae, and later Vayssière (1890*b*, 1893), on the basis of further material, defined the species sufficiently to separate it from both *foliaceum* and *de guernei*. It might be remarked, however, that Eaton's choice was in some ways unfortunate, as *variegatum* differs from three at least of the other species (*foliaceum*, *wouterae* and *africanum*) by possessing the remnant of a sixth gill.

Mention should also be made of the fossil insects described by Brodie (1845) from secondary deposits in England, that were considered by him as having very much the appearance of *Prosopistoma* and by Joly (1871) as " perfectly recognisable" as this insect. There is, however, little to suggest in Brodie's figures that they are other than imperfectly preserved Coleoptera.

A systematic account of the genus and of the two new species from Tanganyika and Natal follows, and the opportunity is taken to re-define the generic characters of the nymph in the light of the greater number of species now known. I must record my indebtedness to Mr. D. E. Kimmins of the British Museum (Natural History) for helpful discussion of several points and to Mrs. C. A. O'Brien for her drawings, reproduced here as figures 1–4.

2. SYSTEMATIC ACCOUNT OF THE GENUS *Prosopistoma*.

Prosopistomatidae Lestage, 1917.

Containing a single genus, *Prosopistoma*, known from the Palaearctic, Oriental and Ethiopian regions and Madagascar.

Prosopistoma Latreille, 1833.

Very small mayflies of fugitive adult existence showing marked sexual dimorphism, suppression of the final ecdysis in the female, reduction in wing venation and partial atrophy of the legs; the nymph an inhabitant of lotic environments, with great enlargement of the mesonotum in the form of a carapace, the tails very short and retractile within the abdomen.

Head in male rather wide; antennae exceptionally well developed, their bases approximating to the mid-line and the second segments separated only by as much as their own width; basal segment small, wider than long and mounted on a prominent sub-median pedestal; second segment enormously enlarged and bottle-shaped, its long axis only slightly shorter than diameter of oculus; filament fine, twice length of second segment. Ocelli large, widely spaced; oculi simple, rather small but nevertheless prominent owing to their origin from stalked lateral projections of the head. Posterior margin of head everted to form a narrow vertical lip extending between the bases of the oculi. Clypeus well formed and prominent from below, in shape rounded and disc-like and projecting forwards ventral to, and appearing between, basal antennal segments.

Head in female lacking posterior marginal lip. Antennae small, widely separated and on basal pedestals; first segment small, second segment shaped as in male but much smaller. Eyes small.

Male thorax.—Pronotum short, considerably broader than long, saddle-shaped; prosternum very wide. Mesonotum squat, ratio of length : breadth 1·3 : 1; scutellum prominent, forming a well-developed median projection. Fore legs short; coxite prominent and rotated outwards; trochanter elongate and projecting laterally; femur flexed at trochanteric joint so as to emerge on the dorso-lateral aspect of the thorax, tibia held in reversed flexion at femoral joint so that the tibia and tarsus are directed backwards, above and lateral to the notum; proportions of femur : tibia : tarsus 3 : 2 : 1; tarsus with two segments, the first completely fused with the tibia and discernible only as a constriction; claws apparently fused to form a single functioning structure. Mid and hind legs partly atrophied, hind legs slightly the longer; femora attenuated and sharply bent distally; effective length of femora about equal to tibiae and three times that of tarsi, these with two segments and poorly differentiated claws. Wings four, membrane slightly opalescent and reinforced with a system of longitudinal creases associated with the main veins; wing margin fringed with fine hairs. Fore wing relatively wide and evenly rounded, ratio of length to maximum breadth 1·8 : 1; venation greatly reduced, forks of all long veins detached at wing root except main fork of R_s; distal portion of R_2 weak and detached, main trunk of R_2 being transferred apparently to another vein from the R_s complex; all remaining eight veins simple, with regular alternation of high and low veins; cross veins entirely absent but in stigmatic area a feeble longitudinal thickening of the membrane visible. Hind wing small, obovate and with prominent right angled costal spur; main veins ill developed, simple and interspersed with fine creases; wing fringe extending on to distal one-third of anterior border, i.e., as far as termination of R_1.

Female thorax.—Pronotum relatively large; mesonotum broad, ratio of length : breadth 1·1 : 1, this broadness accentuated by the enlarged lateral processes of the pronotum; notum in lateral view humped, the mesonotum with a distinct median keel broadening out anteriorly into a sharp beak that overlaps the pronotum. Legs partly atrophied; femora normal, tibiae and tarsi fused to form an indefinite remnant. Fore wing narrower than in male, basal third of posterior margin being parallel to anterior margin and ratio of length to maximum breadth 2·2 : 1; longitudinal veins more strongly developed and wing membrane entirely without creases; distal portion of R_2 not detached (as in male) but failing to reach apex of wing and less strongly developed than the lower branch which extends right up to wing margin. Hind wing narrower and costal spur less prominent than in male; longitudinal veins distinct, forming three main series with moderately deep forks.

Abdomen in male elongate, tapering and feebly chitinised; first segment inapparent, postero-lateral margins of seventh to ninth segments produced backwards as spines; ninth segment wider in antero-posterior diameter than preceding segments, the genital forceps arising from a small protuberance on its ventral aspect; these rather stout in dorso-ventral aspect, thin and attenuated in lateral view; with three segments, basal segment broad, second segment twice as long as first and swollen at apex, third segment broad and pyriform and arising from inner aspect of second segment below the apex so as to leave a broad notch between the tips of the two segments. Penes simple, fused except at tip and arising somewhat posterior to forceps base, so that, although appreciably shorter than the forceps, yet appearing to extend almost to distal forceps segments. Tails three, the median subequal, about half body length and covered with relatively long, coarse setae.

Abdomen in female extremely short and stumpy; first segment inapparent, sixth segment rather deeper than the rest, seventh and eighth tergites with acute postero-lateral spines;

ninth sternite extending backwards to form a broad, entire subanal plate, overlapping tenth segment. Tails three, the median subequal, only equalling about one-tenth of body length and lacking coarse marginal setae.

Male subimago much as imago. All legs apparently functional; fore coxite on ventral aspect of sternum and not rotated outwards, mid and hind femora straight. Wing venation and membrane creases as in imago. Abdomen much shorter, tergal spurs shorter and blunter; genitalia well differentiated but stumpy. Tails equalling about one-tenth of body length.

Head of nymph flattened and narrow; antennae with five segments, second segment the longest. Mouthparts bounded below by the mentum, which is enormously enlarged and plate-like, bearing a deep median notch in front below the labium; labrum small; mandibles tapering to a heavily chitinised, narrow, tri-dentate outer canine, inner canine[1] rather smaller, cylindrical and bi-dentate, bearing at its base a number of long fine setae; molar region of mandible absent; lacinia of maxilla heavily chitinised and terminating in four very strong curved spines, from the base of which a number of long, finely serrated hairs arise; inner border of lacinia with a single very small seta; maxillary palp slender and with three segments, the second segment the longest; labium a simple fused plate, narrower at its base and chiselled out along the lateral margins so as to fit snugly into the median notch of the mentum; labial palp slender with three segments, basal segment the longest or subequal to second segment; hypopharynx absent.

Thorax.—Mesonotum enormously enlarged to form a rounded carapace, convex above with a narrow median ridge and flattened lateral flanges; anterior margin excised to fit closely with head, posterior margin straight or concave and overlapping abdomen as far as base of seventh tergite, its mid point shallowly excised to mark the exhalant aperture of the branchial chamber. Wing buds enclosed within carapace. Underside flattened, prosternal suture well marked, suture between meso- and metasternum absent; coxites arising from shallow depressions which extend backwards and receive the femora when folded. Hind leg rather the longest; fore femur bearing a few very small spines, fore tibia with an armature of serrated spines on the distal half, or rather more, of the inner surface; other legs lacking spines, claws simple and slender.

Abdomen overlapped anteriorly by notal carapace; first segment not distinguishable, second to sixth tergites forming floor of branchial chamber, posterior margin of sixth tergite raised up to form a ridge fitting closely with the posterior margin of the carapace; second to sixth sternites fused with, and completing, the flattened undersurface of the carapace, two inhalant slits present at the junction of the notal flanges with the lateral borders of fourth and fifth sternites. Gills five in number (six in *P. variegatum*), overlapped above by hind wing buds; first gill narrow and ribbon-like, inner border intersected by long digitate processes, second gill a large rectangular lamella overlying third to fifth gills, which are small and each composed of 6–10 fine digitations. Lateral margins of seventh and eighth segments produced backwards as broadish flattened spines; ninth segment narrow and tubular above, broad, flattened and projecting backwards below, with lateral margins flattened and projecting but fused behind with the sternite; tenth segment very small, sternite split almost completely down the mid-line, retractable within the ninth segment. Tails three, equalling about one-seventh to one-eighth of body length and heavily fringed with long hairs on inner and outer borders.

Type species: *P. variegatum* Latreille.

Prosopistoma africanum sp. n. (figs. 1–3, 5–16, 18, 20, 22).

Male imago (fresh). A delicate, mainly white insect. Head sooty; basal half of second antennal segment amber, distal half reddish-brown; eyes black. Pronotum sooty, meso-

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[1] Considered by some authors to be the prostheca or lacinia mobilis.

notum and sternites sandy brown ; in front and slightly below anterior wing root is a small, sharp horizontal projection made conspicuous by its dark brown colour ; recurrent membrane of wing extending as a fine, filamentous projection from the tip of the scutellum as far as the base of the fifth tergite. Fore leg purplish-brown throughout, anterior border of femur marked by a line of 18–22 delicate, recurved hairs ; anterior margin of tibia rugose. Wings generally opalescent, this more marked and tinged with purplish-brown in costal and subcostal areas and basally ; main veins pale ; costal process of hind wing tinged with brown. Abdomen white and distended with air ; terminal segments in life tinged with pink, apparently imparted by the contents of the seminal vesicles. Forceps white ; penes simple, strongly tapered, particularly in the antero-posterior plane, terminating in a narrow bifid apex ; penis tips separated by a median notch extending to about one-third length of penes ventrally but dorsally to only half this distance. Tails white.

Female adult (*subimago*). A short, squat, sombrely-coloured insect. Head and thorax dark purplish brown ; antennal segments brown, filament colourless. Wings generally milky, anterior and basal areas tinged with brown ; veins dark brown. Recurrent membrane projecting beyond scutellum as in male. Abdomen and tails dark brown, the former tinged with yellow from the enclosed eggs.

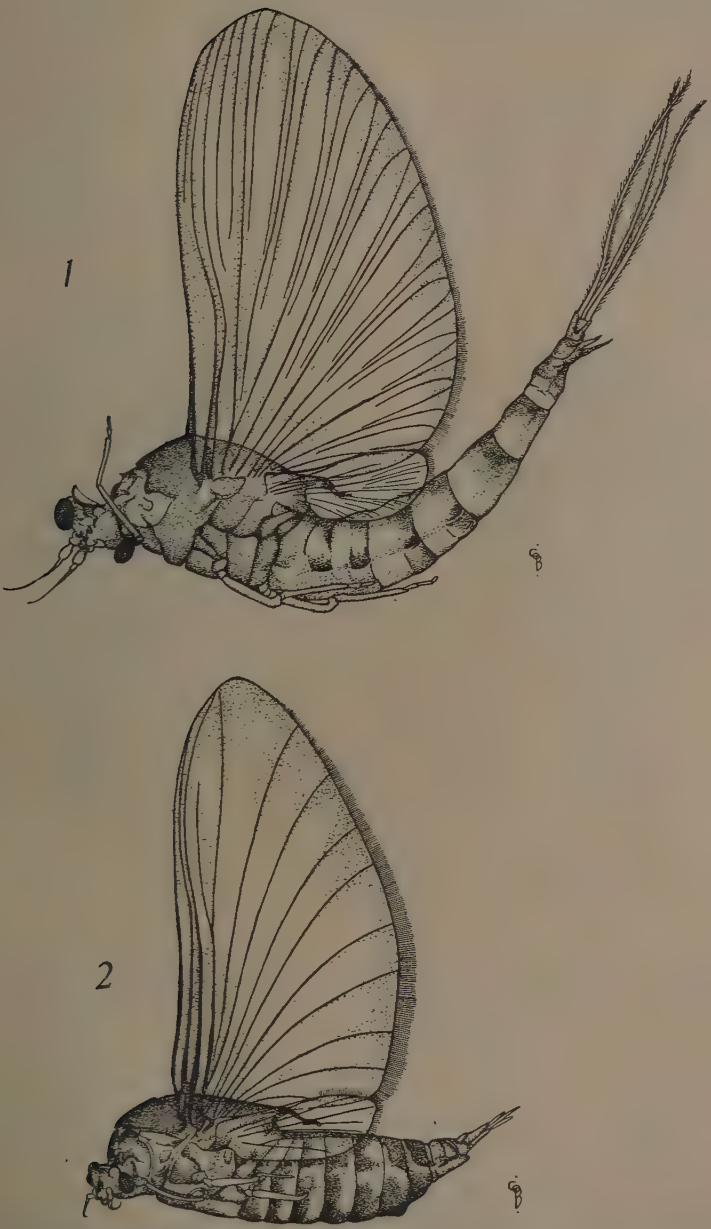
Male subimago.—Colouring much as in imago. Fore leg brownish mauve, the femur lacking marginal fringe of hairs and the tibia not rugose ; other legs colourless. Wings slightly more cloudy than in imago, borders rather more heavily fringed. Abdomen and tails white.

Nymph.—General colour in life chestnut brown with paler markings ; carapace marked with a pair of pale lateral spots at the junction of mid and posterior thirds and usually with an additional pair of pale dashes on either side of the mid-line between the outer spots ; integument finely pitted. Antennae moderately long and extending beyond anterior margin of head ; second segment cylindrical and shorter than third to fifth segments together. Outer canine of mandible slender with 4 or 5 fine teeth on inner margin below apex, inner canine with 4 fine teeth below apex ; 3 hairs arising from base of inner canine, the two distal hairs with the finest possible serrations, third hair apparently simple, and a single long hair arising from the middle of the outer border of mandible ; sub-apical area of lacinia of maxilla with 3 simple hairs, none serrated ; anterior lip of labium without hairs but very finely corrugated in median area, basal segment of labial palp about twice length of second segment ; anterior margin of mentum finely corrugated, except in median notch, and clothed in extremely fine hairs. Thoracic carapace relatively narrow and lateral flange reduced, length along median ridge 1–1·1 times maximum breadth. *Legs* : anterior margin of fore femur with a line of short hairs with the finest possible serrations ; fore tibial armature composed of 6–7, occasionally 5 or 8, spines each bearing 9–10 fine teeth on inner margin, the most distal spine being one-and-a-quarter to one-and-a-half length of preceding spine ; fore tarsus occasionally with one or two simple spines.

Body length : male, 4·8 mm., female, 3·6 mm., male subimago, 4·2 mm. *Wings :* male, 3 mm., female, 4·5 mm. *Tails :* male 2·4 mm., female 0·3 mm.; male subimago, 0·4 mm. *Nymph*, total length, mature male, 2·8–3 mm., female, 3·5–4 mm.

East Africa, Tanganyika : Sigi river, Amani (5° 5′ S., 38° 40′ E.), iv.1951 to vi.1953. The material comprises 46 male imagines, 1 male subimago, 6 females and about 70 nymphs. The holotype (nymph) and a series of adults and nymphs have been presented to the British Museum (Natural History).

This species differs from *crassi* and *de guernei* by the carapace length being equal to or greater than its maximum width, and from *variegatum* by the greater length of the antennae. It is closest to *Prosopistoma* sp. Paulian, from which it differs by the second antennal segment being shorter than segments 3–5 together, by the character of the fore tibial armature, the proportions of the segments of the labial palps and by the unserrated hairs in the maxillae. The

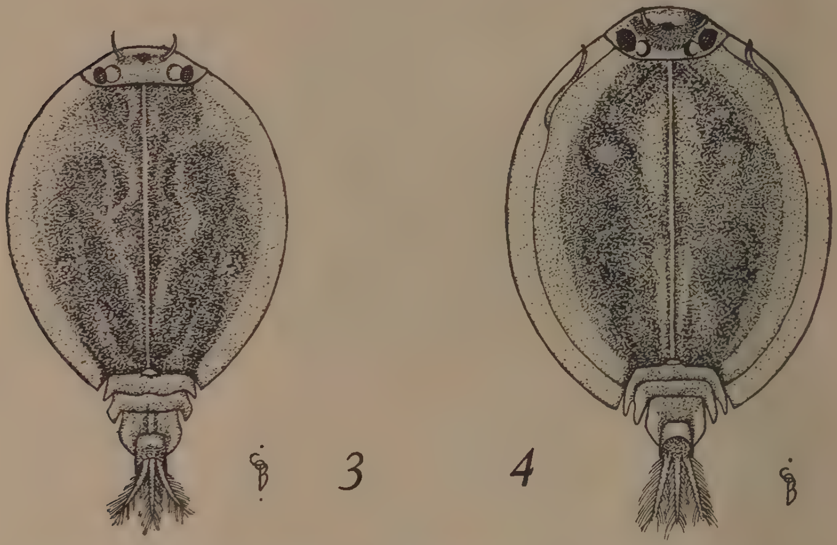


Figs. 1–2.—Adults of *Prosopistoma africanum* sp. n. (1) ♂ imago ; (2) ♀ subimago.

female adult apparently differs from that of *foliaceum* by the extension of the recurrent wing membrane some way beyond the tip of the scutellum.

Prosopistoma crassi sp. n. (figs. 4, 17, 19 and 21).

Nymph.—A moderately large species, pale greenish-brown when preserved in spirit; carapace marked with a pale lateral margin round inner side of flange, rest of area dark except for one or two indefinite pale areas along median suture, the posterior such area being much the smaller; integument finely pitted. Antennae short, not quite reaching anterior margin of head; second segment cylindrical and about as long as third to fifth segments together. Canine region of mandible strongly developed, 2 small heavily chitinised teeth on outer margin immediately below apex of outer canine, inner margins of both canines with 1–2 fine sub-apical teeth, 2 long and 1 short hair arising from base of inner canine, all coarsely serrated, and a single long hair arising from outer margin of mandible; lacinia of maxilla with 3 slender hairs, none serrated (or so finely serrated as not to be detectable); anterior lip of labium without hairs or corrugations, basal segment of labial palp about twice length of second segment; anterior margin of mentum finely corrugated, except in median notch, and clothed with extremely fine hairs. Thoracic carapace broad and lateral flange well developed, length along median ridge 0·8–0·9 times maximum breadth. *Legs*: anterior margin of fore femur with very fine unserrated hairs; fore tibial armature composed of 8–10 spines each bearing 7–9 teeth on inner margin only, the most distal spine not longer than preceding spines. Abdominal tergites sparsely covered with very fine hairs, lateral processes of seventh and eighth segments rather long and posterior margins of these processes coarsely corrugated.

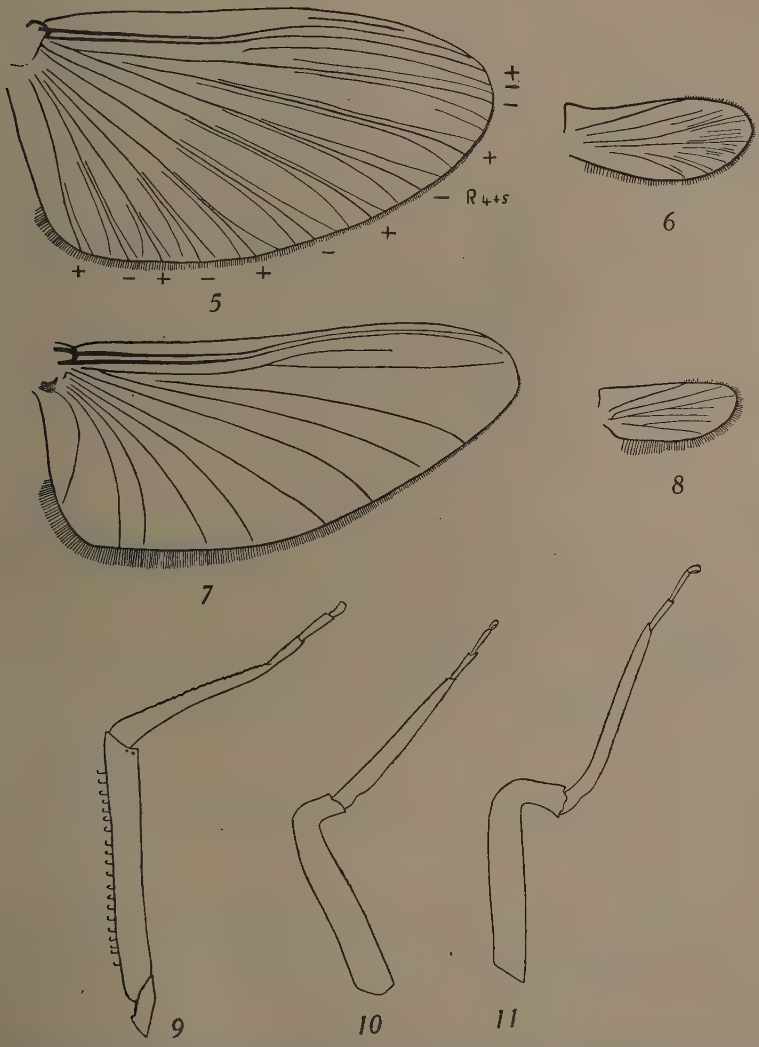


Figs. 3–4.—Nymphs of *Prosopistoma*. (3) *P. africanum* sp. n.; (4) *P. crassi* sp. n.

Total length (mature nymph, probably female) 5·5 mm.; maximum width 3·5 mm.

Holotype nymph, 2 paratypes, South Africa, Natal : Umgeni river (29° 30′ S., 30° 30′ E.), 1200 feet, xii.1953, (*R. S. Crass*). 1 nymph, Tugela ferry (28° 75′ S., 30° 30′ E.), 12.xi.1953 (*W. D. Oliff*). Holotype in British Museum (Natural History).

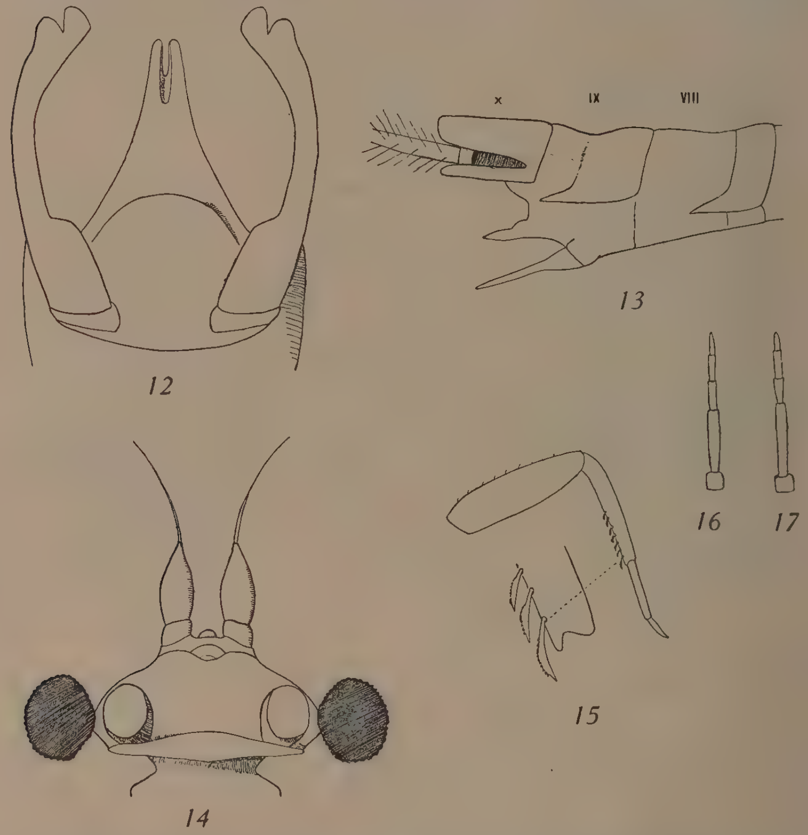
This species differs from all other *Prosopistoma* except *de guernei* by the width of the carapace exceeding that of its length. From *de guernei*, which



Figs. 5–11.—Details of *P. africanum* adults. (5) ♂ fore wing ; (6) ♂ hind wing ; (7) ♀ fore wing ; (8) ♀ hind wing ; (9) ♂ fore leg ; (10) ♂ mid leg ; (11) ♂ hind leg.

was described from a single immature nymph, it should be distinguishable by the much shorter antennae. It was discovered some years ago by Mr. R. S. Crass, for whom I have pleasure in naming it.

With the list of species of *Prosopistoma* described from the nymph now amounting to seven, it is possible to assess the value of some of the taxonomic characters used. The relative proportions of the carapace are clear cut and easily measured, and it has been observed in *P. africanum* that the ratio of length to breadth is remarkably constant even in the smallest nymphs (1–1·5 mm.) measured. For this reason, Vayssière's conclusion (1936) that the breadth of the carapace in the type specimen of *de guernei* from Senegal was simply the result of its immaturity, and that the specimens with quite different dimensions from Mount Elgon in Kenya were attributable to the same species, cannot be accepted. The Kenya species must be considered distinct and as yet inadequately described.



Figs. 12–16.—*P. africanum.* (12) ♂ genitalia from below; (13) ditto, lateral view; (14) Head, ♂ imago; (15) Nymph, fore leg; (16) Nymph, antenna; (17) *P. crassi* nymph, antenna.

The markings on the carapace are also important and will probably be found to be distinctive once a sufficiently large series of each species is available. In over 50 *P. africanum* examined, the two lateral pale areas were nearly always present, and it was only in completely mature specimens that these markings were occasionally obscured by the dark colour of the adult within. On the head, the total length and proportions of individual segments of the antennae form another easily determined character, although in *africanum* occasional apparently malformed specimens are seen with only four segments. Similarly, the character of the fore tibial spines—“ armature ” seems an appropriate term—is also very valuable. In all except the very smallest specimens of *africanum* their number was constant at 6–7 or occasionally 5 or 8 spines, and within certain limits their number alone may be a useful guide. In addition, the presence of teeth on one or both sides of the spines, the number of teeth on each spine and the relative length of the ultimate spine all seem to vary between species. In the mouthparts, useful characters may be found in the number of teeth on the stalks of the canines, the number and serrated nature of the accessory hairs on the mandibles and maxillae and the proportions of the different segments of the maxillary and labial palps.

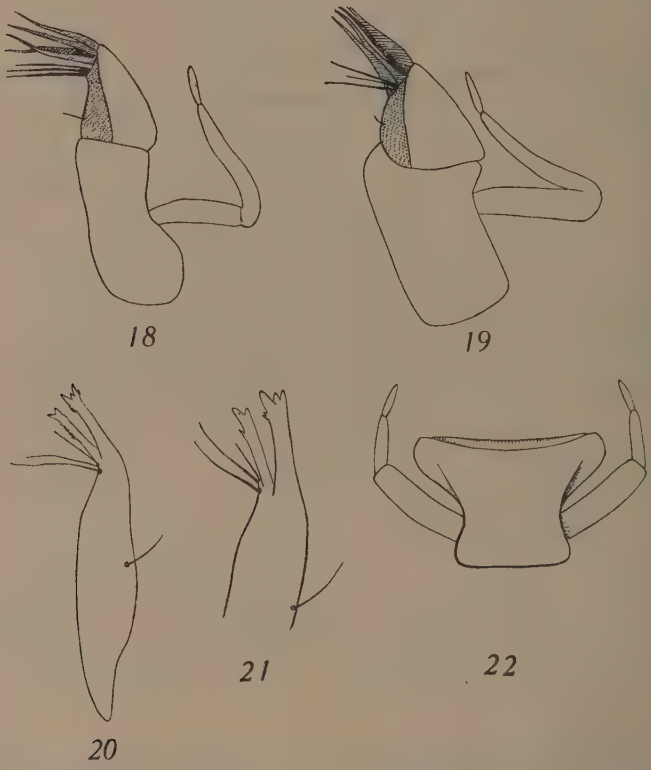
It is clear that many characters are available for the separation of the nymphs of this genus, while the ease with which the adults may be separated is still to be discovered. For this reason, the nymph has been designated as the holotype of *africanum* and no hesitation was felt in describing and naming *crassi* from nymphal material alone. The following key has been prepared and may be of value as a provisional guide to the African fauna as known at present.

1. Carapace length along median suture equal to, or greater than, maximum width 2
–. Carapace length less than maximum width 4
2. Antennae longer than distance between base of antenna and anterior margin of head 3
–. Antennae shorter than distance to anterior margin of head (Madagascar) **P. variegatum**
3. Second antennal segment shorter than segments 3–5 together, fore tibial armature composed of 5–8 spines . . . . **P. africanum**
–. Second antennal segment longer than segments 3–5 together, fore tibial armature composed of 10–12 spines . . . . **Prosopistoma** sp. Paulian
4. Antennae longer than distance between base of antenna and anterior margin of head . . . . **P. de guernei**
–. Antennae not longer than distance to anterior margin of head . **P. crassi**

3. Taxonomic Features of the Adult *Prosopistoma*.

Many unusual taxonomic features are displayed by the adults of *Prosopistoma*. It may be convenient to discuss some of these in greater detail.

Sexual dimorphism.—While the suppression of the final ecdysis in the female undoubtedly accentuates the differences between the sexes, *Prosopistoma* shows a far greater degree of dimorphism than has hitherto been recognised within the order. Differences in the eyes, legs and abdominal appendages are usual amongst the Ephemeroptera, but only in *Tortopus*, Traver (1950), and to a lesser extent *Campylocia*, Ulmer (1942) and Spieth (1943), do these extend to the wing venation. But in *Prosopistoma*, the wings are quite different in both shape and venation in the two sexes. In the forking of the R_s complex in the fore wing, R_2 is detached but complete in the male, intact but incomplete in the female, and the strongly formed veins of the female contrast with the feebler venation of the male, a weakness apparently compensated for in the male by the development of " creases " parallel to the main veins. The shape and venation of the hind wings are even more divergent. No less striking is the short, plump body of the female, four-fifths or less the length of each wing, and the long relatively insubstantial body of the male, which is more than one and a half times the length of the wings.



Figs. 18–22.—Mouthparts of nymphs. (18) *P. africanum*, maxilla ; (19) *P. crassi*, maxilla ; (20) *P. africanum*, mandible ; (21) *P. crassi*, mandible ; (22) *P. africanum*, labium.

Antennae.—The extraordinarily large and bottle-shaped second antennal segment in the male is almost without parallel in the order. The same organ in the female, well figured by Vayssière (1881*a*, *b*), is of similar shape, but much smaller and the antennae have not converged towards the mid line.

Legs.—As far as can be made out, the peculiar conformation of the fore legs of the male imago has resulted from the following structural modifications: (i) prominence and outwards rotation of the fore coxite; (ii) slight elongation and lateral projection of the trochanter; (iii) fixed flexion of the femur at the trochantero-femoral joint, and (iv) reversal of the femoro-tibial joint. In this way, the legs project onto the dorso-lateral aspect of the thorax and are apparently incapable of extension in any other direction. This is presumably an adaptation for mating. In most Ephemeroptera in which the male seizes the female from below, the legs are elongated and curve backwards over the head, Needham, Traver and Hsu (1935, fig. 13); but the male of *Prosopistoma* appears to achieve the same power of grappling with quite short legs by bringing them up on either side of the thorax, surely a unique type of specialisation! Observation of the actual mating position assumed would be valuable.

Wings.—The wings are characterised by the elimination of all cross veins and the deepening and detachment of all forks beyond R_s, so that all veins behind this are simple and a very perfect system of fluting has developed. Thus interpretation of the homologies of the main veins posterior to the sector fork is difficult. The simple alternation of high and low veins makes clear that this pattern has not simply resulted from the disappearance of intercalary veins to leave the main branches of MA and MP intact. It is suggested tentatively that IMA and MA_2 (using the system of nomenclature outlined by Tillyard, 1932) may have been lost and that the veins represented posterior to R_{4-5} are respectively MA_1 (+), MP_1 (—), IMP (+), MP_2 (—), CuA (+), CuP (—) and A_1 (+). In the hind wings there is also great reduction in venation, but less so in the female than in the male, in which the intermingling of fine veins with creases in the membrane makes interpretation almost impossible.

The wing membrane in the male is unique for the development of a system of longitudinal thickenings or " creases " in association with the main veins. Their distribution is very constant, but their precise structure or origin for the moment remains obscure. It is possible that they are similar to the creases observed in certain Diptera, for example Blepharoceridae or Deuterophlebiidae. On the other hand, the rather broader longitudinal band of thickening in the stigmatic area in the male may perhaps have been derived from anastomosis and fusion of marginal veinlets.

Abdomen.—The final ecdysis in the male is accompanied by lengthening of the abdomen. The distension of the gut with air and the extreme thinness and delicacy of the integument suggest that some degree of extension and thinning of the segments occurs at this stage. The first abdominal segment cannot be distinguished for certainty in either sex, but the possibility of its existing as a narrow basal ridge cannot be excluded. The forceps appear quite stout when seen from below but in lateral view it is seen that the terminal segments are thin and flattened. The penes are apparently fused except at the extreme apex.

Comparison of the female of *P. africanum* with Vayssière's description of *foliaceum* shows that there is close similarity between the two forms and that his figures and description of all organs, with the notable exception of the wings, must be accepted as accurate and adequate. As suggested by him, and confirmed in the present work, there is every reason to believe that the subimago is the ultimate stage in the female, and he was therefore perfectly correct in his claim to have discovered the " perfect state " of that particular sex.

4. SYSTEMATIC POSITION OF *Prosopistoma*.

Prosopistoma is a specialised mayfly, long separated from the main stem of development of the Ephemeroptera. As specialised features one may mention the antennae in the male, partial atrophy of the legs with reduction in the number of tarsal segments to two, the extreme simplification of the wing venation and the complete elimination of all cross veins, the fused penes and reduction in the length of the tails. The structure of the nymph is well known and one need only mention the mesonotal carapace, branchial chamber and retractile tails as evidence of its specialised character.

Apart from a superficial resemblance of the adults to *Caenis*—a resemblance which is not confirmed by close examination of any individual structure—*Prosopistoma* is quite remote from the adults of all other Ephemeroptera. It only remains to consider how far the undoubted similarity of the nymphs of *Baetisca* and *Prosopistoma* is paralleled in the adults and whether these affinities reflect genuine phylogenetic kinship. Lestage (1917), on the basis of nymphal characters, placed both these insects in the same group of Cryptobranches, and Lameere (1917), a few months later, was also so impressed by the similarities between them that he placed them together in the same family, Prosopistomidae. Apart from nymphal structures, he considered that certain characters in the wings of the adults indicate their common origin. He mentioned, in particular, the shape of the wing with long posterior border and basal position of the anal angle, the closely parallel course of CuA, CuP and A_1 before their termination *distal* to the anal angle and the fact that this last character is found in no other recent Ephemeroptera. These arguments cannot, however, be fully accepted now. The male wing resembles in shape that of *Caenis* as much as *Baetisca*, and, in interpreting the homologies of the veins of *Prosopistoma*, Lameere was misled by the indefinite nature of Vayssière's figure of the wing to locate the veins posterior to R_2 too far forward, so that the last vein called by him fourth anal was, in fact, the third anal ($= A_1$); this terminates, in the female, posterior to the anal angle and thus differs from *Baetisca* and resembles other Ephemeroptera. But it is true, nevertheless, that CuA and CuP run a more or less parallel course in both these insects and in no other mayflies except the fossil *Hexagenites*, figured by Eaton (1871) and Handlirsch (1908). In other respects the wings show wide differences and, apart from a superficial similarity between the genitalia of the two genera, the adult stages of *Baetisca* and *Prosopistoma* show few signs of close relationship.

The nymphs on the other hand have many structural features in common, notably a mesonotal carapace, branchial chamber and the cephalisation of the central nervous system, and these have been regarded as evidence of the close relationship of the two forms. The relationship does not, it should be noted, extend to at least one important taxonomic character—the mouthparts. The general facies of the adults suggests to the present writer that the relationship between the two forms is remote. Nevertheless, it is hard to see how the simultaneous development of similar structures in the nymphs and in the wings of the adults, as shown by the unique arrangement of the cubital veins, could result from the parallel development of two distinct stocks under the influence of similar environmental pressures. For this reason, it must be concluded that both forms are derived from a common stock of great antiquity, but that since then evolution and specialisation have proceeded independently.

5. Biology of *Prosopistoma africanum*.

P. africanum is relatively abundant in streams belonging to the Sigi River system of the Eastern Usambaras. These mountains form a narrow range of ancient crystalline rocks, bounded by steep escarpments, some 20–30 miles inland from the East African coast at Tanga; they rise to a maximum height of between 4000 and 5000 feet. They are noted for the luxuriance of the rain forest that covers much of the uncleared areas and for the presence of relict and endemic elements in the fauna and flora (Moreau, 1935, 1952). *Prosopistoma* nymphs occur in some of the smallest streams as little as one or two feet across, as well as in the main Sigi river, and have been found at all altitudes between 700 and 2800 feet; the former figure, it may be noted, is now near the lower limit of the forest. They were found in greatest numbers in the 1500–2200 feet zone of the main river, but they also occurred not uncommonly in an overgrown forest stream at the lower altitude limit in water in which hot season temperatures of 80–84° F. were regularly recorded.

The nymphs harbour on the underside of rocks or under quite small stones at depths varying from 2 inches to 3 feet, in reaches where the current is rapid or moderate and where sand and silt are not deposited. As a rule they are not found in the most torrential stretches, but their presence at greater depths or under rocks too big to move cannot be excluded. The catching of 10–12 nymphs in the course of an hour's searching was considered to indicate local abundance, but it was not unusual to turn over many rocks without result and then to find several nymphs close together under the same stone. Other insects associated with them included *Euthraulus* (an undescribed species), undetermined Baëtidae, Psephenid larvae, *Helicopsyche* and *Neoperla*. *Prosopistoma* nymphs were found at all times of the year and it is possible that the emergence season varies with altitude. Mature nymphs were, however, found in June at 900 and 1500 feet and in January at 700 and 2200 feet. Their tolerance to static water in the laboratory is surprising; specimens can often be kept alive in corked specimen tubes overnight with only few deaths, and one nymph survived for two weeks under these conditions without even the water being changed. No evidence was obtained about their feeding habits, but, as Lestage (1925) pointed out, their carnivorous potentialities must still be considered unproven. Doubts might also be raised over the frequently repeated statement that *Prosopistoma* is an active and efficient swimmer. It is true that in captivity the nymphs swim with elegance and rapidity, and it is a pleasure to watch their active gyrations when first captured and placed in still water. But anyone who has watched their helplessness when placed in a gauze cage in running water must be struck by the ill adapted nature of such a flattened bodily form to free swimming in a current, and it seems unlikely in nature much use is made of this form of progression.

The capture of the first adults was facilitated by the fortunate chance that the first serious attempt at breeding out from nymphs coincided with the emergence season at the 2000 feet level (water temperatures from a few observations 70–75° F.), where a natural swimming pool in the Sigi river at the base of a waterfall provided a convenient and attractive site for collecting nymphs. These were transferred to a gauze breeding-out cage maintained in a small concrete tank constructed by the side of a stream at Amani (2900 feet) and fed with water direct from it. The first adult emerged within a week, and during the course of a month three females and a male were bred out in this tank and another male (a subimago) obtained in the laboratory. During the months of January and February ten visits were made to the river in the vicinity of the swimming pool, at and soon after dawn, and on seven mornings adult *Prosopistoma*, mostly males, were caught on the wing over the river. Adults were only seen during the 45 minutes immediately following daybreak, between 06.15 and 07.00 hours (East African Standard Time), and it seems likely that emergence is at dawn and that their entire adult existence is encompassed within this short period of time. Females obtained from the emergence cage showed no inclination to shed the subimaginal pellicle and were identical in appearance with those caught on the wing in nature. These wild caught females fluttered without intermission after capture until water was introduced into the tubes that confined them; this led to the instant deposition of eggs. Thus it is practically certain that the subimago represents the final adult female and that they are precluded by atrophy of the legs from ever settling again or from indulging in any other activity beyond this single nuptial flight. There was, it may be added, no evidence that the pellicle was shed in flight.

The first male to be obtained was found in the emergence cage trapped by its wings in the subimaginal shuck. A second male bred in the laboratory in a specimen tube was unable to escape and died still a subimago, thus establishing the existence in the male of the normal subimaginal and imaginal phases. All males caught in nature were imagines. They fly with a peculiar jerky side-to-side motion, quite unlike the usual graceful dancing of mayfly spinners, and form close-knit little swarms from 6 to 12 feet above the river, that drift slowly down stream and are often hard to see in the early morning light. Occasional individuals are seen at lower levels. After capture, like the females, they continue their efforts to fly, their fore legs held grotesquely above and beside the thorax.

The adults, particularly the males, are extremely delicate insects and their bodies rapidly become dried up and shrivelled. In collecting material, it was found necessary to wait until a number of specimens had been collected in the net at one time before tipping them all without handling direct into 70 per cent. spirit. Similarly, in examining material under the microscope, dense mounting media such as balsam or polyvinyl alcohol cannot be used for examining the abdominal appendages, owing to the crushing and distortion that results.

Eggs were obtained from one or two females caught in nature. These were yellow in colour, not much longer than broad and with a rugose and apparently sticky outer layer of, or secretion from, the chorion. This layer appeared to be detachable and was absent from one pole of the egg in all specimens examined. With this qualification, the general appearance is much as figured by Vayssière (1881*a*, *b*). They are laid separately, but tend to stick to the bottom and to each other subsequent to laying and rapidly become covered with detritus. Egg batches were kept in bowls of water in the laboratory for up to two months without hatching of larvae being observed.

This inevitably superficial study of the biology of *P. africanum* has shown that in behaviour it does not differ in any major respect from other Ephemeroptera. It shares with *Palingenia*, Schoenemund (1930), but not apparently *Campsurus*, the suppression of the final ecdysis in the female. Morgan's account (1929) of the mating flight in the latter genus is not quite clear on this point. While the total limits of the flight period for the species as a whole are very restricted, it is possible that the life of an individual *Prosopistoma* is not very much shorter than, for instance, *Caenis*. If this same flight period is common to other species, it might be suggested that adults of *foliaceum* should be sought soon after daybreak in early summer over the rivers of Europe where nymphs have been found. The presence of *africanum* in small streams, and the abundance and relative hardiness of the nymphs, have undoubtedly simplified the study of this species, and this has made it possible, even in the limited time available for this work, for some progress to be made towards a fuller knowledge of this elusive insect.

6. Summary.

An account is given of the hitherto very imperfectly known adult of *Prosopistoma*, based on a collection of adults and nymphs made in Tanganyika. Two new species are described from East and South Africa respectively. The taxonomy and systematic position of the genus are discussed, and some notes are given on the biology and behaviour of the East African species.

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A REVISION OF THE *LUGUBRIS* COMPLEX IN THE GENUS *MELIGETHES* STEPHENS (COLEOPTERA: NITIDULIDAE).

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Manuscript received 5th October, 1953.

(Read 5th May, 1954.)

With 22 Text-figures.

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INTRODUCTION.

Reitter, in 1919, defined the relatives of *M. lugubris* Sturm in his 7th Group of the *Meligethes* as those in which the outer edge of the front tibiae towards the apex is crenulate or finely toothed, with two larger more prominent teeth interposed, the more proximal being near or somewhat before the middle of the outer edge, the more distal close to the apex, and the tibia itself gradually widened from the base to the proximal large tooth and thence more or less parallel-sided as far as the distal.

Within this larger group, however, may be recognised a smaller complex of species, much more closely related to *lugubris*, in which the elytra, at least near the sides and base, show a fine cross-striation or feeble transrugosity, combining with this character a common form, more or less oval, somewhat strongly narrowed in front and behind, with the head slightly produced anteriorly giving the impression of a short snout, a markedly convex under-surface (except in *acicularis* Brisout), a uniform more or less shining deep black colour, and the presence in the male of secondary sexual characters both on the metasternum and on the last ventral segment of the abdomen. To be excluded from this smaller group are *M. subfumatus* Ganglbauer, which, though its elytra are cross-rugose, is more elongate, is furnished with longer closer pubescence, is not so deep black, and has a simple last sternite in the male, and *M. fumatus* Erichson, which, though of the same general form as *lugubris*, is clothed with long yellowish pubescence hiding its non-rugose upper surface, has pale reddish-yellow legs and antennae, and likewise lacks secondary sexual characters on the last ventral segment.

TRANS. R. ENT. SOC. LOND. 105. PT. 16. (NOVEMBER 1954). 21

Amongst the members of this *lugubris* complex the distinguishing characters are often small and obscure. Nevertheless, in conformity with a previous decision (1951), I regard them not merely as botanical sub-species (cf. Deville, 1908 : 233), but as being worthy each of full specific status.

KEY TO THE SPECIES OF THE *LUGUBRIS* COMPLEX OF THE GENUS *MELIGETHES.*

1. Much less convex above and below, so that the side border of each elytron viewed from directly above is simultaneously visible in its entirety ; more parallel-sided, pronotum not strongly narrowed in front nor the elytra towards the apex ; pronotum more strongly transverse and distinctly narrowed to base, so producing an angulation between its side margin and that of the elytron on each side ; pronotum with surface between the punctures distinctly microscopically reticulate ; elytra less distinctly trans-rugose at sides ; length 1·8–2·0 mm. *Male :* metasternum moderately deeply impressed posteriorly, without a median longitudinal raised ridge ; last sternite with a median very small shining tubercle close to the apex ; tegmen of aedeagus (fig . 1) with prominent lateral lobes curved outwards ; median lobe of aedeagus (fig. 2) simple, without longitudinal raised ridges on the dorsum. *Female :* ovipositor (fig. 15) somewhat long and sharp, with the suture between the coxites and valvifers more or less straight. Germany, North France, Central Europe, Asia Minor
acicularis Brisout (= *angulosus* Rebmann) (p. 377).

Much more convex above and below, so that the side border of each elytron viewed from directly above is not simultaneously visible in its entirety ; less parallel-sided, more narrowed in front and behind ; pronotum less strongly transverse, generally less narrowed to base, so that there is a less well developed angulation between the sides of pronotum and elytron ; pronotum with surface between the punctures usually smooth on the disc ; elytra more distinctly transrugose at the sides. *Male :* metasternum with a median longitudinal raised ridge or tubercle ; last sternite with secondary sexual character more highly developed, never a simple round tubercle ; median lobe of aedeagus (figs. 4–14) with two longitudinal, somewhat convergent, shining, raised ridges on the dorsal surface . . . . 2.

2. Somewhat more parallel-sided ; upper surface between the punctures entirely smooth ; with an extremely feeble bronze reflection ; length 1·9–2·3 mm. *Male :* metasternum in the posterior half triangularly impressed and with a low median longitudinal ridge ; last sternite with a slightly raised shining transverse ridge curved with the concavity posteriorly ; tegmen (fig. 3) with large lateral lobes curved inwards, the apical excision being deep and parallel-sided. *Female :* ovipositor (fig. 16) with the suture between coxites and valvifers inversely V-shaped. Western Mediterranean region, Hungary
submetallicus Deville (p. 378).

More narrowed in front and behind ; upper surface between the punctures not always non-reticulate ; quite black. *Male :* tegmen of aedeagus (figs. 5–13) with lateral lobes smaller and not strongly curved ; metasternum with a prominent longitudinal tubercle at its centre ; last sternite with a much more strongly raised large tubercle or transverse ridge close to the apex. *Female:* ovipositor with the suture between coxites and valvifers almost straight and transverse (figs. 17–22) . . . 3.

3. Surface of elytra between the punctures smooth and shining, or microscopically reticulate. *Male:* tegmen of aedeagus (figs. 5, 7 and 9) with lateral lobes much smaller and somewhat square and with apical excision shallow (that of *morulus* is unknown). *Female:* in the species with reticulation of the surface of the elytra the ovipositor is entirely reddish yellow (that of *nitidicollis* is unknown) . . . . 4.

Surface of elytra between the punctures always microscopically reticulate. *Male:* tegmen of aedeagus (figs. 11 and 13) with lateral lobes much longer and bluntly pointed, and apical excision deeper. *Female*: ovipositor with deep black pigmentation . . . . 9.

4. Surface of elytra between the punctures distinctly microscopically reticulate . . . . 5.

Surface of elytra between the punctures smooth, or with fine strigae running from puncture to puncture, not microscopically reticulate . . 6.

5. Broader oval; upper surface of pronotum between the punctures entirely smooth. *Male:* last sternite bearing two prominent transversely-placed keel-like tubercles; aedeagus very similar to that of *lugubris*. *Female*: ovipositor unknown. East Siberia, Mongolia, Japan

nitidicollis Reitter (p. 379).

More elongate oval; surface of pronotum between the punctures microscopically reticulate over a wide area in front of and around each basal sinuation. *Male;* last ventral segment of abdomen having a strongly raised transverse keel before the apex; aedeagus unknown. *Female:* ovipositor (fig. 17) entirely reddish yellow, without dark pigmentation. Japan . . . . **mikado** Reitter (p. 380).

6. Robust, short oval; upper surface between the punctures entirely smooth; with fine dark pubescence; length 2 mm. South Africa

morulus Reitter (p. 382).

More elongate; if length less than 2·15 mm. then with more conspicuous pale pubescence, or with the upper surface of elytra having fine strigae running from puncture to puncture. Europe, Western Asia, North Africa . . . . 7.

7. More elongate and more parallel-sided, as *acicularis* and *submetallicus*; with longer and more conspicuous pubescence. *Male:* tegmen of aedeagus (fig. 9) with lateral lobes more rounded and less distinct, with the apical excision very shallow. *Female:* ovipositor (fig. 18) with the " central point " quite central, and with the outer subdivision of the coxites more elongate and reaching nearer to the apex. Length 1·9–2·15 mm. North Africa . . . . **normandi** sp. n. (p. 382).

Less elongate, less parallel-sided, more strongly narrowed towards front of pronotum and apex of elytra; pubescence shorter and less conspicuous. *Male:* tegmen of aedeagus (figs. 5 and 7) with lateral lobes more squared and prominent, and with apical excision deeper. *Female:* ovipositor (figs. 19 and 20) with the " central point " slightly nearer the apex, and with outer subdivision of the coxites shorter. Europe, Western Asia . . . . 8.

8. Length 1·6–2·1 mm.; less convex and less shining; punctures of elytra much less distinct, scarcely larger than the eye facets and separated by about three diameters; surface of elytra with microscopically

distinct strigae running between the punctures; with microscopic reticulation between the punctures at the base of the pronotum. *Male:* metasternum much more strongly and closely punctured, with the median keel shorter and less prominent; ridge on last ventral segment much narrower than hind tibia, consisting of two shining tubercles separated by a concavity, seen in profile it slopes evenly forwards and backwards, behind it the hind edge of the segment is excised; aedeagus (figs. 5 and 6) less elongate, tegmen with the apical excision deeper and the lateral lobes more prominent. *Female:* ovipositor (fig. 19) having the suture between coxites and valvifers straight, the basal edge of each coxite being transverse. Host-plant: *Thymus serpyllum* L. . . . . **lugubris** Sturm (p. 385).

Length 2·1–2·5 mm.; more convex and more shining; punctures of elytra much more distinct, appreciably larger than the eye-facets and separated by about two diameters; surface of elytra between the punctures smooth; without or with very faint microscopic reticulation between the punctures at the base of the pronotum. *Male:* metasternum much less strongly and closely punctured, and with the median keel longer and more prominent; ridge on last ventral segment of abdomen scarcely less wide than the hind tibia, straight and overhanging posteriorly, so that in profile the hind slope is markedly concave, behind this the hind edge of the segment is simple; aedeagus (figs. 7 and 8) more elongate, tegmen with apical excision shallower and lateral lobes less prominent. *Female:* ovipositor (fig 20) having the suture between coxites and valvifers in the form of a very flattened V, the basal edge of each coxite running obliquely in an apical direction from the " central point." Host-plants: *Mentha* spp. . . . **gagathinus** Erichson (p. 385).

9. Less shining, microscopic reticulation between punctures of elytra always distinct; legs very slightly broader; edge of metasternum opposite hind trochanter very strongly raised in male, moderately strongly in female. *Male:* metasternum with a central longitudinal ridge and a triangular depression occupying the hind half; last ventral abdominal segment with a central blunt tubercle on the posterior aspect of which is a tuft of dark pubescence, and behind this is a smooth area as wide as the hind edge of the metasternum; tegmen of aedeagus (fig. 11) with apical excision bluntly V-shaped with sides divergent. *Female:* ovipositor (fig. 21) shorter with apex less acute, and with the " central point " appreciably nearer to the apex. Europe, Asia
egenus Erichson (p. 387).

More shining, microscopic reticulation between punctures of elytra much less distinct; legs very slightly narrower; edge of metasternum opposite hind trochanter very feebly raised in male, not at all in female. *Male:* metasternum with a tubercle in front of the centre, and a triangular depression occupying the hind two-thirds; last ventral segment of abdomen with a central transverse raised ridge, on the posterior aspect of which is a tuft of dark pubescence, and behind this is a smooth area distinctly less wide than the hind edge of the metasternum; tegmen of aedeagus (fig. 13) with apical excision U-shaped with sides sub-parallel. *Female:* ovipositor (fig. 22) more elongate with apex more acute, and with the " central point " centrally placed. North Africa . . . . **otini** sp. n. (p. 388).

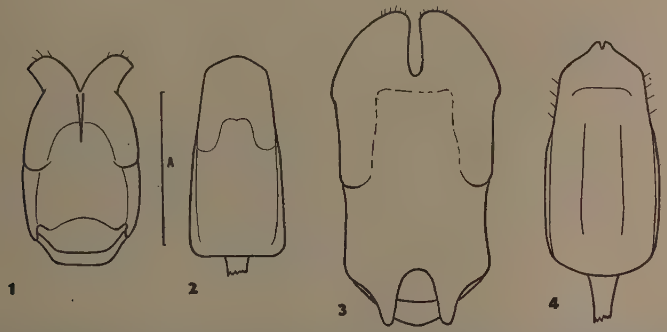
DESCRIPTIONS OF AND NOTES ON THE SPECIES.

Meligethes acicularis Brisout (= *angulosus* Rebmann).

Meligethes angulosus was described by Rebmann in 1940 from a unique male taken in Asia Minor. Later (1943) he recognised the same species as occurring in Germany.

He had been prevented by the World War from comparing his insect with the type of *M. acicularis* Brisout (1863), a specimen from Northern France, and in enumerating the distinguishing characters had been obliged to rely upon his wide experience of " *M. acicularis* " from the Mediterranean region.

I have recently examined a paratype (♀) of *M. acicularis* from Lardy (S. et O.) and find it not only identical with examples of *angulosus* kindly lent me by Herr Rebmann, but specifically distinct from the Mediterranean insect regarded by various authors since 1871 as *acicularis*.



FIGS. 1–4.—Aedeagi. (1) Dorsal view of tegmen of *Meligethes acicularis* Brisout. (2) Dorsal view of median lobe of *M. acicularis*. (3) Tegmen of *M. submetallicus* Deville. (4) Median lobe of *M. submetallicus*. Scale A = 0·25 mm.

It was this latter, (though he was not aware that it was other than the true *acicularis* Brisout) which was recognised by Deville in 1920 as being identical with what he had previously (1908) described as the variety *submetallicus* of *lugubris* Sturm. Being unable to find evidence of the use of any other name for this insect, I declare *M. submetallicus* Deville as the legitimate name by which it must now be known, with the synonymy of the two species as follows :

M. acicularis Brisout, 1863,
angulosus Rebmann, 1940.

M. submetallicus Deville, 1908,
acicularis Rebmann, 1940 *et auctt.*,
nec Brisout, 1863.

Rebmann (1943) believed the host-plant of his *angulosus* to be *Stachys recta* L., and it is noteworthy that this plant favours calcareous ground and is recorded from Rouen, where I have myself taken the beetle. However *Thymus serpyllum* L. grows in similar localities, and was one of the very few plants recorded by Rebmann as growing in the restricted area at Sandhausen where he located the beetle. By analogy with the habits of its close relatives it would appear to me more likely that *M. acicularis* would employ as its host this latter plant, more nearly related to *Mentha* than is *Stachys recta*. The question must remain open until such time as the larva may be tracked down.

Meligethes submetallicus Deville.

A brief history of the use of the name *submetallicus* has been given in the above section. Having regard to the very cursory account given by its author, the following fuller description of the species is made from examples collected by Mr. J. H. Harvey at Hyères (Var) in May, 1949.

Male.—Length, 2·1; breadth, 1·05 mm. Elongate, not strongly narrowed in front and behind, somewhat strongly convex, deep black, shining, with fine short inconspicuous greyish pubescence; legs black, the front tibiae very slightly reddish. *Head* transverse triangular, very feebly convex. Clypeus with its anterior margin widely, somewhat deeply, emarginate, its side angles sharp. Surface with punctures equal to, or slightly smaller than, the eye facets, and separated by a half to one diameter, the spaces between the punctures smooth. Antennae with the basal segment brownish black, the second brownish, the third to the eighth and the club almost black; club nearly twice as long and a little more than twice as wide as the first antennal segment. *Pronotum* transverse, a little more than one and a half times as wide as long (1·0 : 0·6 mm.), widest at the basal two-fifths, with sides weakly rounded and convergent towards the front. Anterior margin almost evenly concave, the blunt obtuse front angles not strongly prominent. Hind margin longer than the front (0·95 : 0·55 mm.), almost straight, but very feebly sinuate on either side of the scutellum; hind angles obtuse and bluntly pointed. Sides extremely narrowly bordered. Surface with punctures twice as large as those of the head, separated by half a diameter, the narrow spaces between entirely smooth and shining. *Elytra* slightly longer than broad (1·1 : 1·05 mm.), widest at the basal third and here very slightly wider than the pronotum; sides extremely narrowly bordered, the border visible only at its ends when viewed directly from above, gently rounded and somewhat more convergent posteriorly towards the widely rounded hind angles; the apex of each elytron transversely somewhat strongly curved, sutural angle obtuse-angulate. Shoulders feebly prominent. Surface with punctures showing well-marked transverse rugosity throughout, but most evident at the base; punctures slightly coarser than those of the pronotum, elongate and becoming more shallow towards their hind end, separated by about one diameter, the spaces between smooth and shining. *Scutellum* triangular with rounded apex; its shallow punctures about equal to those of the head, separated by one to two diameters, the surface between being transversely reticulate. *Pygidium* with surface granular, finely and densely punctate. *Ventral surface* black, shining, moderately convex. Prosternal process gradually broadened to its rounded apex, close to which it is one and a half times as wide as the antennal club; its deep punctures coarser than the eye facets and separated by a half to one diameter, the surface between the punctures smooth. Metasternum with punctures shallower and finer than those of the prosternum, separated by about one diameter, the somewhat rugose surface between them finely reticulate; with distinct fine pubescence; the male secondary sexual characters take the form of a well-marked triangular depression the base of which corresponds to that of the metasternum, its apex being at the centre of the latter; traversing this triangle is a median longitudinal ridge the hind end of which is raised as a low tubercle. Abdomen with all segments extremely finely and moderately diffusely punctured, with the surface between finely reticulate; pubescence fine but distinct. The caudal marginal line of the hind coxal cavity follows closely the posterior edge of the latter, turning backwards just before reaching its outer end. The last ventral segment exhibits shortly in front of the middle of its hind edge a low raised shining transverse tubercle almost equal in width to the antennal club, feebly concave posteriorly, and behind this is a row of dense straight yellowish recumbent pubescence. *Legs* almost black, front tibiae and intermediate and hind tarsi slightly reddish, segments one to four of front tarsi yellowish brown. Front tibiae strongly broadened from base to middle, then feebly so to just short of the apex, where it is strongly contracted to the tarsal insertion. Outer edge extremely feebly crenulate to the middle, then with a small sharp prominent tooth separated by three or four very small teeth from a second more prominent but blunter tooth close to the apex, a final small tooth intervenes between this and the somewhat narrow subtarsal plate. Intermediate tibiae not strongly broadened, widest at the middle, outer edge somewhat evenly rounded and furnished from the basal third with a row of very close short stout spines. Hind tibiae narrower than the intermediate, widest at the apical fourth, the inner edge weakly convex, the outer in its apical half with a row of close short fine spines. Front tarsi moderately dilated, slightly wider than the antennal club ; intermediate tarsi just wider than, the hind equal to, the first antennal segment ; last segment of all tarsi shorter than the first four together ; claws simple. *Genitalia* as figured (figs. 3 and 4). Tegmen having the appearance of a cloven hoof, its apical excision long narrow and parallel-sided, its lateral lobes large with their outer edges convex and convergent to the apex. Median lobe slightly constricted at, and narrowed from, the apical third, and having the apex distinctly acuminate ; furnished on the dorsum with a pair of sub-parallel raised ridges.

Female.—In this sex the front tarsi are scarcely broader than, the intermediate and hind equal to, the first antennal segment. Both metasternum and the last ventral abdominal segment lack the secondary sexual characters noted in the male. Ovipositor as figured (fig. 16). This organ is characteristic and peculiar in that the suture separating coxites and valvifers is not almost straight as in other species, but inversely V-shaped, the " central point " of the organ being nearer the apex than the outer ends of the suture ; the apex is sharp and pigmented.

Plesiotype.—Male in my collection, taken on *Cistus*, FRANCE : Hyères, 7.v.49. (*J. H. Harvey*). Other specimens in my collection were taken on various flowers in the same locality and on the same date.

Comparative notes.—In general appearance this species very closely resembles *M. lugubris* Sturm, from which however, as from *gagathinus* and *normandi*, it is at once distinguished in both sexes by an examination of the genitalia. Than *acicularis* Brisout it is much more convex and much more shining, whilst its pronotum is less transverse and shows no trace of reticulation of its upper surface. The smooth surface of its elytra and other external characters readily differentiate it from *egenus* and *otini*. Systematically it is clearly more closely related to *lugubris*, *gagathinus*, and *normandi*, to *egenus* and *otini*, than to *acicularis*, a fact which I have attempted to emphasise in the above key.

Biological notes.—My own examples of *M. submetallicus* Deville were taken on a wide variety of plants, none of which is likely to have been its true host. It seems justifiable to postulate that it is attached to a *Mentha* or closely related botanical species.

Meligethes nitidicollis Reitter.

Meligethes nitidicollis, described by Reitter in 1872 (1873) from Manchuria, was subsequently reported by him (1919) as occurring also in Japan, Eastern Siberia, and Mongolia. Reitter was aware of its close relationship to *M. lugubris* Sturm and distinguished it by its broader form, the closer, finer, punctuation and less distinct transrugosity of its upper surface, and especially by the microscopic reticulation between the punctures of its elytra. Moreover the last ventral segment in the male bore two transversely placed very distinct sharp conical tubercles, much larger than those of *lugubris*, which in this species he recognised as little more than the prominent ends of a short transverse ridge.

In 1940 Rebmann reported the results of examination of two examples of *M. nitidicollis*, of which one bore a determination label in Reitter's handwriting, sent to him on loan from Hamburg by Herr Sokolowski. He considered the external differences, including the well-marked male secondary characters on the last sternite, to be within the limits of variation, and found on dissection an aedeagus which in his view was identical with that of *lugubris* Sturm and of *gagathinus* Erichson. He concluded that all three were one and the same species.

These specimens of *M. nitidicollis* Reitter were unfortunately lost (Rebmann *in lit.*) during the bombing of Hamburg in July 1943, and I have not been able to trace other authentic examples for personal consideration. My own view, hereinafter expressed, as to the specific distinctness of *M. lugubris* Sturm and *M. gagathinus* Erichson, leads me to the further conclusion that *M. nitidicollis* Reitter too is a good species, especially in view of its distinctive male abdominal appendage, and of the well-marked microscopical reticulation of the surface of its elytra.

From *M. mikado* Reitter, the other Far-Eastern species of the *lugubris* complex, it is apparently distinguishable by its broader form, by the entirely smooth upper surface of its pronotum, and by the form of the appendage on the last ventral segment of the male.

Meligethes mikadò Reitter.

The original very inadequate description of *M. mikado* formed part of a key to the Japanese species published by Reitter in 1884, though in the following year a slightly fuller account appeared, which included details of the male secondary sexual character on the last ventral segment of the abdomen. It is unfortunate that on neither of these occasions did the author make any comparison with, or allusion to, *M. nitidicollis* Reitter from Manchuria, and again in 1919 when he noted the close relationship of the latter to *M. lugubris* Sturm that he should have overlooked, and failed to mention, the equally close affinity of *mikado*. This omission is the more perplexing as at this date Reitter included Japan within the range of *nitidicollis*. It is just possible, though there is no record on the point, that Reitter had come to consider *mikado* and *nitidicollis* as identical.

Until such time as authentic specimens can be compared it would seem desirable, on the basis of the characters noted in the above key by which their descriptions differ, still to regard the species as distinct.

A single female example collected in Japan by G. Lewis, and bearing a Type label, and the name "*micardo*" in Reitter's handwriting, stands in the general collection of the British Museum (Natural History). From this specimen the following augmented description of the species is made.

Female.—Length, 2·4; breadth, 1·3 mm. Elongate oval, somewhat strongly convex, deep black, the elytra having a faint metallic reflection, with short, not very conspicuous, yellowish pubescence; legs black. *Head* transversely triangular, slightly convex. Clypeus with anterior margin widely emarginate, its side angles sharp. Surface with punctures equal in size to the eye facets and separated by half a diameter, the very narrow spaces between apparently smooth. Antennae with the first segment black, the second reddish-yellow, the six following progressively more piceous, the club black ; club small, one and a half times as long and twice as wide as the first antennal segment. *Pronotum* moderately transverse, somewhat less than twice as wide as long (1·15 : 0·6 mm.), widest at the basal fourth, with sides gently rounded and more convergent towards the front. Anterior margin straight for the width of the neck, curving forward somewhat strongly at each end to the blunt obtuse front angles. Hind margin longer than the front (1·1 : 0·7 mm.) almost straight, but with a sinuation on either side of the scutellum ; hind angles obtuse. Sides extremely narrowly bordered. Surface with punctures equal in size to those of the head, separated anteriorly by one diameter, towards the base by one and a half diameters ; the spaces between the punctures smooth in the fore part, but very distinctly microscopically reticulate for a wide area in front of and around each basal sinuation. *Elytra* slightly longer than broad (1·45 : 1·3 mm.), widest at the middle, and here distinctly wider than the pronotum ; sides very narrowly bordered, evenly gently rounded, and convergent posteriorly towards the widely rounded hind angles ; the apex of each elytron transverse and feebly curved, sutural angle obtuse. Humeral prominences distinct. Surface with punctures showing slight transverse rugosity at base and sides ; punctures at base slightly finer than those of the pronotum and separated by two to three diameters, shallower and slightly more diffuse towards the apex ; the spaces between the punctures distinctly microscopically reticulate throughout. *Scutellum* triangular with apex rounded ; minutely reticulate throughout ; anterior two-thirds impunctate except for a few scattered shallow depressions at the extreme base, behind this finely, closely, but irregularly punctate. *Pygidium* with surface granular, very finely and closely punctured. *Ventral surface* black, moderately strongly convex, fore parts shining, abdomen slightly duller ; with short dark pubescence. Prosternal process strongly broadened, widest just in front of its almost truncate apex, and here twice as wide as the antennal club ; its punctures quite twice as wide as the eye facets, deep and somewhat elongate, separated by a half to one diameter, absent from a narrow band along the hind margin ; surface between the punctures smooth. Mesosternum unpunctured, reticulate. Metasternum somewhat convex, with punctures finer than those of the prosternal process, slightly larger than the eye facets, and separated by two to three diameters, with a broad band along the hind margin unpunctured ; surface between the punctures smooth. Abdomen with the first sternite having punctures equal in size to the eye facets, separated by two to three diameters ; the remaining four segments progressively more finely and closely punctured, with the surface between obscurely reticulate. The caudal marginal line of the hind coxal cavity at first deviates backwards very feebly, as in *gagathinus*, then rejoins the hind edge of the cavity shortly before turning back close to its outer end. *Legs* black. Anterior tibiae strongly broadened from base to middle, then parallel-sided almost to the apex, here two-fifths as broad as long ; outer edge very feebly but gradually more evidently crenulate to the middle, where is the proximal more prominent tooth ; beyond this are on the one side two, on the other three, smaller teeth, followed by the distal larger and more prominent tooth situated just before the apex, and between this and the narrow subtarsal plate is a single smaller tooth. Intermediate tibiae not strongly broadened, widest in the middle, outer edge evenly rounded and furnished from the basal fourth with short close spines. Hind tibiae widest at the apical fourth, with inner edge evenly feebly convex, outer edge rounded at apex, furnished from the basal third with close downwardly directed spines, slightly longer and finer than those of the intermediate pair. Front tarsi feebly dilated, one and a half times as wide as the first antennal segment ; last segment of all tarsi slightly shorter than the first four together ; claws simple. *Genitalia* as figured (fig. 17). Ovipositor entirely reddish-yellow, without any piceous pigmentation ; with the " central point " centrally placed, and the suture between coxites and valvifers transverse ; somewhat abruptly narrowed to the apex.

Type ♀, Japan (*G. Lewis*). In British Museum (Natural History).

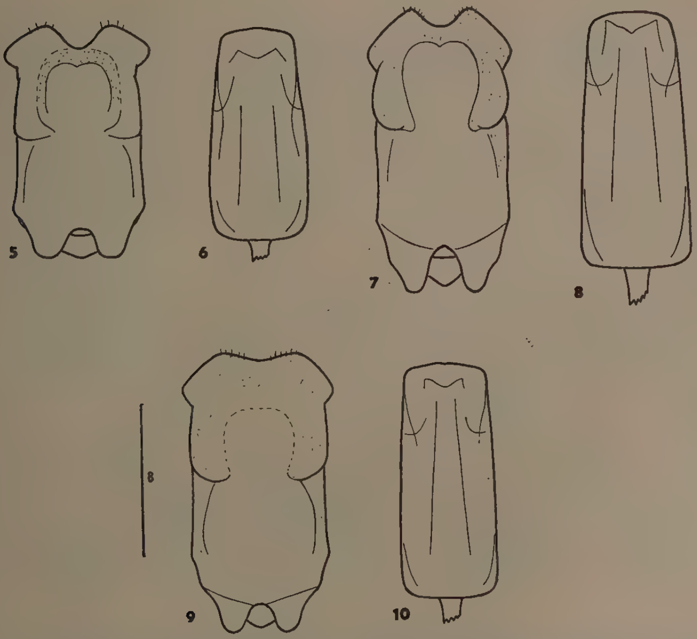
Comparative notes.—Even if not identical with *M. nitidicollis* Reitter, *M. mikado* is clearly very closely related to it as to those other four species, *lugubris* Sturm, *gagathinus* Erichson, *morulus* Reitter, and *normandi* sp. n. with which these two have been segregated in the above key. From them it is at once distinguished by the microscopic reticulation of the surface of its elytra; moreover its ovipositor lacks any dark pigmentation, and is more elongate with its apex more abruptly narrowed than is the case in these species (the ovipositor of *morulus* is unknown). From *egenus* Erichson it is at once separated by the simple hind edge of its metasternum opposite the hind trochanter, and from both this species and *otini* sp. n. by the absence of black pigment from its ovipositor. This organ is likewise amply distinct from those of *acicularis* Brisout and *submetallicus* Deville.

Meligethes morulus Reitter.

M. morulus is unknown to me, and was described by Reitter in 1872 from a single female example taken at the Cape of Good Hope. From *M. gagathinus* he distinguished it by the position of the proximal more prominent tooth above the middle of the outer edge of its front tibia, and from *lugubris* by its closer and finer punctuation and entirely smooth upper surface.

Meligethes normandi sp. n.

Male.—Length, 2·2; breadth, 1·1 mm. Elongate, not strongly narrowed in front and behind, moderately strongly convex, deep black, shining, with moderately long, slightly conspicuous yellowish pubescence; legs black, the front tibiae somewhat reddish. *Head* transverse, triangular, feebly convex. Clypeus with its anterior margin widely, somewhat deeply, emarginate, its side angles sharp. Surface with punctures slightly larger than the eye facets, and separated by half a diameter, the spaces between the punctures smooth. Antennae, except the brown second segment, black; club nearly twice as long, and a little more than twice as wide, as the first antennal segment. *Pronotum* transverse, not quite twice as wide as long (1·0 : 0·55 mm.), widest at the basal two-fifths, with sides moderately rounded and more convergent towards the front. Anterior margin straight for the width of the neck, curving forwards slightly at each end to the blunt obtuse front angle. Hind margin longer than the front (0·95 : 0·55 mm.), slightly convex and feebly sinuate on either side of the scutellum; hind angles obtuse and slightly rounded. Sides extremely narrowly bordered. Surface with punctures equal in size to those of the head, separated by half to one diameter, the spaces between smooth, except close to the basal sinuations where there is a faint trace of reticulation. *Elytra* longer than broad (1·15 : 1·1 mm.), widest at the middle and here very slightly wider than the pronotum; sides very narrowly bordered, gently rounded and somewhat more convergent posteriorly towards the widely rounded hind angles; the apex of each elytron transversely somewhat strongly curved, sutural angle obtuse. Shoulders feebly prominent. Surface with punctures showing slight transverse rugosity throughout; punctures equal in size to those of head and pronotum, though slightly elongate, separated by one and a half to two diameters, but somewhat finer and more diffuse at the extreme apex, where the surface between shows a trace of microscopic reticulation, being smooth elsewhere. *Scutellum* triangular with rounded apex; moderately coarsely and closely, but shallowly punctate, with the surface between the punctures reticulate. *Pygidium* with surface granular, finely and closely punctate. *Ventral surface* black, somewhat shining. Prosternal process gradually broadened to its rounded apex, where it is one and two-thirds times as wide as the antennal club; its deep punctures coarser than the eye facets and separated by half a diameter;



FIGS. 5–10.—Aedeagi. (5) Dorsal view of tegmen of *Meligethes lugubris* Sturm. (6) Dorsal view of median lobe of *M. lugubris*. (7) Tegmen of *M. gagathinus* Erichson. (8) Median lobe of *M. gagathinus*. (9) Tegmen of *M. normandi* sp. n. (10) Median lobe of *M. normandi* sp. n. Scale B = 0·25 mm.

surface between the punctures smooth. Mesosternum unpunctured, reticulate. Metasternum in front very finely and diffusely punctured, but in the posterior half with punctures only slightly finer than those of the prosternal process and separated by one and a half to two diameters, a broad band along the hind margin unpunctured; surface between the punctures smooth; the male secondary sexual characters consist of a sharp longitudinal raised ridge in the midline extending from the centre to the posterior fourth, the surface of the metasternum in its hind half is triangularly flattened, and its edge opposite the hind trochanters is very slightly raised. Abdomen with all sternites extremely finely punctured, the first very diffusely, the second to fifth more closely, surface between the punctures microscopically reticulate. The caudal marginal line of the hind coxal cavity follows the posterior edge of the latter, turning backwards shortly before reaching its outer end. The last ventral segment exhibits just in front of the middle of its hind edge a raised transverse ridge the length of which equals the maximum width of the hind tibia, the central portion of this ridge is deeply excised so that its ends appear as two shining tubercles; seen in profile the edge of the ridge overhangs posteriorly, there being a marked concavity between it and the hind edge of the segment; the latter is slightly emarginate in the middle. *Legs* very nearly black, front tibiae reddish, segments one to four of all tarsi pitchy yellow. Front tibiae strongly broadened from base to middle, parallel-sided to apical fifth, then strongly contracted to tarsal insertion; outer edge very finely crenulate to the middle, then with a small sharp prominent tooth separated by three very small teeth from a second more prominent tooth at the apical fifth, which is again separated by a smaller tooth from the narrow subtarsal plate. Intermediate tibiae not strongly broadened, widest in the middle, outer edge more or less evenly rounded and furnished with close fine spines. Hind tibiae widest at the apical fourth, with inner edge feebly convex, outer edge in its apical half set with a row of close spines finer and slightly longer than those on the intermediate tibiae. Front tarsi moderately dilated, just appreciably wider than the antennal club; intermediate tarsi as wide as the first antennal segment, hind tarsi slightly narrower; last segment of all tarsi slightly shorter than the first four together; claws simple. *Genitalia* as figured (figs. 9 and 10). Tegmen with the apical excision extremely shallow and the lateral lobes much reduced, almost rounded, but with an oblique flattening representing the squared ends exhibited by *lugubris* and *gagathinus*. Median lobe sub-parallel, with apex somewhat abruptly rounded off; with a pair of longitudinal raised ridges on the dorsum.

Female.—Differs from the male externally in the following characters: the anterior tibiae are less dilated, being parallel-sided in the apical half where their width is little more than a quarter of their length; front tarsi not dilated, one and a half times as wide as the first antennal segment; intermediate and hind tarsi as wide as this segment; the metasternum is simple, lacking the male secondary sexual character, and the last sternite is similarly simple. Ovipositor as figured (fig. 18); the " central point " centrally placed with the suture between coxites and valvifers straight; with deep piceous pigmentation.

Type, ♂ TUNISIA: Le Kef, vii.1949 (*Dr. H. Normand*). In the collection of Dr. H. Normand.

Paratypes.—In the collection of Dr. Normand, two females taken in company with the type, five females from Le Kef without date, and one male also from Le Kef dated vi.1936. In the collection of the Institut Scientifique Chérifien, one male from MOROCCO: Ouezzan, 22.viii.1928 (*Théry*). In my own collection, the following specimens taken in ALGERIA: Azazga (*B. Leat*): On *Cistus*, 31.v.53, 1 ♀; on *Mentha pulegium* L., 31.v.53, 4 ♀, 10.vi.53, 1 ♀, 14.vi.53, 1 ♂, 3 ♀, and 28.vi.53, 1 ♀.

Variations.—Little variability is to be noted in the series before me. The smallest measures 1·9 mm. in length, the largest 2·15 mm.

Comparative notes.—*M. normandi* is very closely related to both *M. lugubris* Sturm and *M. gagathinus* Erichson, its numerous small diagnostic characters being best set out in tabular form:

M. normandi sp. n.	*M. lugubris* Sturm.	*M. gagathinus* Erichson.
Length 1·9–2·2 mm.	Length 1·6–2·1 mm.	Length 2·1–2·5 mm.
Somewhat elongate and more parallel-sided.	Less elongate and more narrowed in front and behind.	As *lugubris*.
Less convex, as *lugubris*.	Less convex.	More convex.
Pubescence longer and more conspicuous.	Pubescence shorter and less conspicuous.	As *lugubris*.
Elytra more strongly rugose.	Elytra less strongly rugose.	As *lugubris*.
Elytral punctures coarser.	Elytral punctures finer.	Punctures coarser as in *normandi*.
Surface of elytra between punctures smooth.	With distinct microscopic strigae between the punctures.	Surface of elytra smooth, as in *normandi*.
Surface between punctures at base of pronotum smooth or very nearly so.	Surface between punctures at base of pronotum with distinct microscopic reticulation.	As in *normandi*.
Front tarsus of male more strongly dilated.	Front tarsus of male less strongly dilated.	Front tarsus of male more strongly dilated.

M. normandi sp. n.	*M. lugubris* Sturm.	*M. gagathinus* Erichson.
Metasternum more finely and diffusely punctured.	Metasternum more strongly and closely punctured.	Metasternum more finely and diffusely punctured.
Ridge on last ventral segment of male bi-tubercular.	Ridge on last ventral segment of male bi-tubercular.	Ridge on last ventral segment of male scarcely emarginate.
In profile the ridge is strongly concave posteriorly.	In profile the ridge slopes away gradually posteriorly.	As in *normandi.*
Aedeagus of intermediate length.	Aedeagus less elongate.	Aedeagus more elongate.
Tegmen with apical excision shallower, and lateral lobes more rounded, less distinct and less prominent at the sides.	Tegmen with apical excision deeper, and lateral lobes square and more prominent.	Tegmen with apical excision intermediate, and lateral lobes square and of intermediate prominence.
Ovipositor with "central point" centrally placed, with suture between coxites and valvifers straight, and with the outer subdivision of the coxites more elongate.	Ovipositor with the "central point" situated nearer the apex, with the suture straight, and with the outer subdivision of the coxites shorter.	Ovipositor with the "central point" situated as in *lugubris,* with the suture in the form of a very flattened V, and with the outer subdivision of the coxites short as in *lugubris.*

Biological notes.—Dates of recorded captures of this species are uniformly late in the season, which becomes very hot in North Africa before June. This fact, coupled with the close relationship of the species to *M. gagathinus*, suggests the probability that it too is attached to a species of *Mentha.* Thus there seems no reasonable doubt that *Mentha pulegium* L., on which nearly all the Azazga specimens were taken, constitutes its real host. Confirmatory evidence for this assertion lies in the great preponderance of females found on the plant.

Meligethes lugubris Sturm and *M. gagathinus* Erichson.

Meligethes lugubris was described by Sturm in 1845, and the same year Erichson added *M. gagathinus* as a distinct species. Reitter, too, in his early days (1871) regarded them as distinct, with *M. ebeninus* Förster (1849) as a synonym of *lugubris* Sturm, and *cristatus* Förster (1849) as a synonym of *gagathinus* Erichson.

Subsequent authors, including Brisout (1872), Fowler (1889), Ganglbauer (1899), and Deville (1935–38), regarded *gagathinus* as a variety of *lugubris* and some confusion of the characters of the two ensued. By 1919 Reitter himself had accepted this view, and had likewise confused the characters.

Finally Rebmann in 1940, in his . . . *Bemerkungen zu einigen anderen Arten der* lugubris-*Verwandtschaft*, having dissected a large number of males, concluded that not only were *M. lugubris* and *M. gagathinus* identical, but that *M. nitidicollis* Reitter (1872 (1873)) was also none other than the same species.

For many years, as a result of careful field work combined with morphological studies, I have been convinced as to the distinctness of *M. lugubris* and *M. gagathinus*. For their diagnosis little need be added to the morphological details already noted in the key and in the tabulated characters given above (*vide M. normandi* sp. n.), by a careful consideration of which no difficulty should arise.

The smaller, *M. lugubris*, employs as its host-plant the Labiate *Thymus serpyllum* L. Thus it commonly occurs on limestone and chalk hills, where, besides being found on its host, it may be had by general sweeping, or be taken in flowers such as *Fragaria vesca* L., *Carduus acaule* (L.) Scop., and *Knautia arvensis* (L.) Coult. growing in association with the thyme. The larger, *M. gagathinus*, is undoubtedly attached to various species of *Mentha*. Thus it is more common in the damp situations where the more frequent species of *Mentha* abound, and here it is to be taken by sweeping along the banks of streams or ponds, and in damp situations in woods, or from such flowers as those of *Lycopus europaeus* L. growing in proximity to the mint. Owing however to the occurrence of some species, e.g. *Mentha arvensis* L. on dry chalky hills, the beetle is by no means absent from such localities, a fact of importance in dispelling any idea that *lugubris* and *gagathinus* might be divergent forms of the same species, the result purely of environmental conditions.

Of *M. gagathinus* I have taken the second (final) instar larvae in moderate numbers from the flowers of *Mentha verticillata* L. and from one of them succeeded in rearing the adult. The discovery of the larvae of *M. lugubris* presented greater difficulties, but by introducing the beetle in some numbers to a plant of *Thymus serpyllum* L. growing under cover I have this year obtained several first and one second instar larvae, and more recently a short series of mature larvae has been secured from large picked bunches of flowers of the same plant. This larval material has been preserved and examined with his usual thoroughness by Dr. F. I. van Emden who kindly reports (*in lit.*) that the larvae of *lugubris* are of much darker coloration than those of *gagathinus* associated with more solid paramedian spots on the pronotum and other minor differences, whilst the width of the head capsule varies from 0·375 to 0·43 mm. as compared with 0·43 to 0·47 mm. in the case of the latter species.

M. gagathinus would appear to be commoner than *M. lugubris*, at least in the British Isles; both occur in Western Europe, and probably extend through the greater part of the continent, and into the Caucasus (Reitter, 1877 (1878)) and Siberia (Horion, 1951).

At this point brief consideration may be given to *M. mellitulus* Reitter, described in 1872 from a single example collected in the Rhineland. Neervoort van de Poll (*vide* Ganglbauer, 1899 : 534) regarded it as no more than an exceptionally well-sculptured example of *lugubris*, whilst by 1911 Reitter, basing his opinion on the false premise of the importance of the position of the proximal larger tooth on the outer edge of the front tibiae, believed it to be a form of *gagathinus*. The opinions expressed by Deville (1908), that it might be his *submetallicus*, and by Heymes (Franck, 1934, as quoted by Horion, 1935), that German examples of *acicularis* Brisout were *M. lugubris* v. *mellitulus*, were clearly erroneous and may be discounted. Having considered the facts and the arguments I regard *mellitulus* as a form of *lugubris* Sturm, in accordance with the interpretation of van der Poll.

The synonymy of the two species under consideration may be expressed:

M. lugubris Sturm, 1845,
ebeninus Förster, 1849,
mellitulus Reitter, 1872,

M. gagathinus Erichson, 1845,
cristatus Förster, 1849.

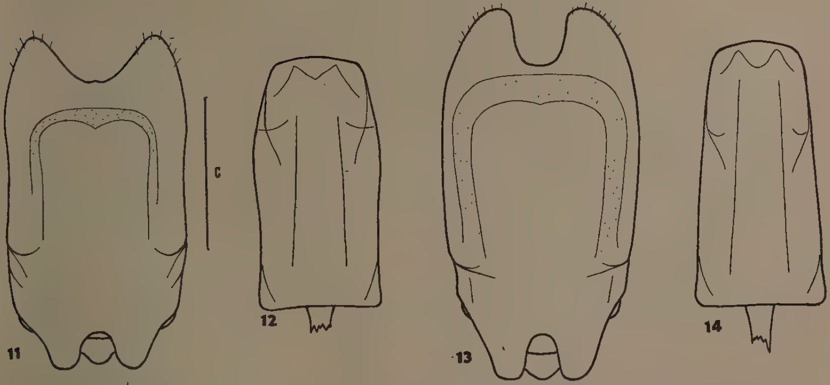
Meligethes egenus Erichson.

This species, established by Erichson in 1845, was re-described in 1863 by Brisout under the synonym *menthae.*

The distinct elevation in the male of the hind edge of its metasternum opposite the hind trochanter was pointed out by Ganglbauer in 1899. To a less degree this character is present also in the female and constitutes a quick and reliable means of differentiation from all other related European species. As already noted in the key it is much less marked in the male of the North African *M. otini* sp. n., and absent in the female.

The microsculpture of the surface of the pronotum is very variable, being usually distinct and covering the whole surface, but at times absent except near the base. The apical excision of the tegmen is normally wide and deep, with the lateral lobes long and sharp, but age and wear may well blunt and reduce these considerably.

M. egenus Erichson occurs widely throughout Europe with the exception of the British Isles, also in the Caucasus and Siberia. Its close attachment to *Mentha* spp. was known to Brisout (1863), Reitter (1875), Perris (1875 (1876)) and to subsequent authors, whilst Gobert (1875-76) recorded the finding of its larvae in flowers of *M. rotundifolia* (L.) Huds. It is probable that this latter species alone constitutes its true host.



FIGS. 11–14.—Aedeagi. (11) Dorsal view of tegmen of *Meligethes egenus* Erichson. (12) Dorsal view of median lobe of *M. egenus.* (13) Tegmen of *M. otini* sp. n. (14) Median lobe of *M. otini* sp. n. Scale C = 0·25 mm.

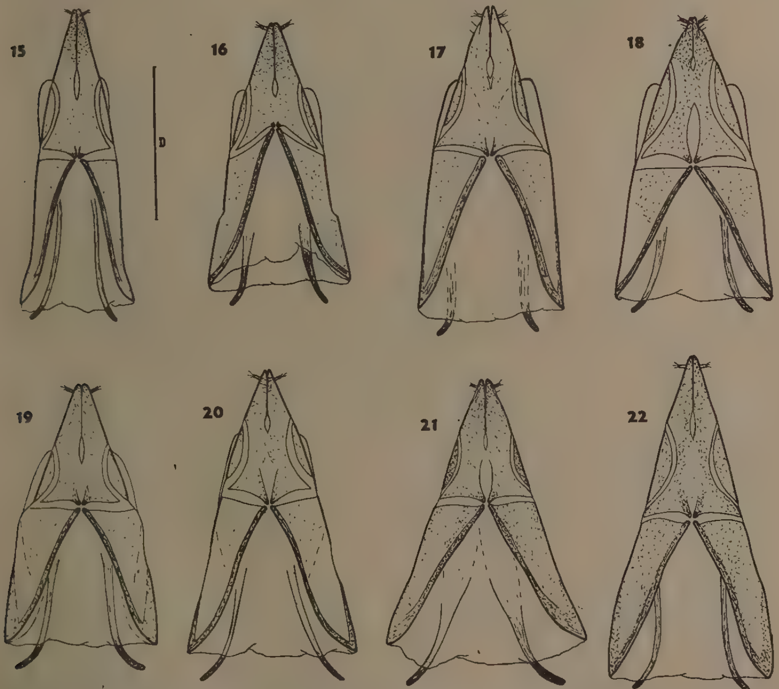
Meligethes otini sp. n.

Male.—Length, 2·1; breadth, 1·1 mm. Elongate oval, somewhat strongly convex, deep black, shining, with short, not very conspicuous, silvery pubescence; legs black. *Head* slightly transverse, triangular, feebly convex. Clypeus with its anterior margin widely emarginate, its side angles sharp. Surface with punctures equal in size to the eye facets, and separated by about half a diameter, the spaces between the punctures smooth. Antennae, except the yellowish second segment, black; club small, one and a half times as long, and twice as wide as the first segment. *Pronotum* moderately transverse, being somewhat less than twice as wide as long (1·05 : 0·6 mm.), widest at the basal third, with sides gently rounded and more convergent towards the front. Anterior margin almost straight for the width of the neck, curving forward slightly at each end to the blunt obtuse front angles. Hind margin longer than the front (1·0 : 0·6 mm.), almost straight, being very feebly sinuate on either side of the scutellum; hind angles obtuse. Sides extremely narrowly bordered. Surface with punctures in the anterior part equal in size to those of the head, becoming gradually slightly larger towards the base, separated by three-quarters to one diameter, the spaces between smooth, except close to the base where they are distinctly microscopically reticulate. *Elytra* slightly longer than broad (1·2 : 1·1 mm.), widest at the middle and here slightly wider than the pronotum; sides very narrowly bordered, evenly gently rounded, and convergent posteriorly towards the widely rounded hind angles; the apex of each elytron transverse and gently curved, sutural angle obtuse. Shoulders moderately prominent. Surface with punctures showing slight transverse rugosity at base and sides; punctures at base slightly coarser than those on the adjacent part of the pronotum, gradually finer towards the apex, separated in the former position by one and a half diameters, and in the latter by two to two and a half diameters; the spaces between the punctures are somewhat wrinkled and show a more or less distinct microscopic reticulation, more obvious towards the apex. *Scutellum* transverse with apex rounded; finely, shallowly, and diffusely punctured, with the surface between distinctly reticulate. *Pygidium* with surface granular, very finely and closely punctured. *Ventral surface* black, fore parts shining, abdomen somewhat dull with more conspicuous pubescence. Prosternal process gradually broadened to its rounded apex, where it is one and two-thirds times as broad as the antennal club; its punctures deep and slightly larger than the eye facets, separated in its anterior part by half to one diameter, but much more diffuse in the posterior third where the intervals are of about two diameters; surface between the punctures smooth. Mesosternum unpunctured, reticulate. Metasternum with punctures slightly coarser than those of the prosternal process, separated by one and a half to two diameters, though rather closer at the sides, and with a broad band along the hind margin unpunctured; surface between the punctures smooth and shining; the male secondary sexual characters consist of a somewhat deep triangular impression occupying the hind two-thirds of the metasternum, and at the anterior apex of this triangle is a well-developed somewhat elongate median tubercle. Abdomen with the first sternite having punctures equal in size to the eye facets and separated by one to two diameters; the remaining four sternites much more finely and closely punctate. The caudal marginal line of the hind coxal cavity follows closely behind the posterior edge of the latter turning backwards shortly before attaining its outer end. The last ventral segment at its centre shows a well-marked sharp transverse ridge, in length slightly exceeding the width of the antennal club, anteriorly this ridge slopes gradually onto the adjacent surface, but posterriorly it drops abruptly and on this aspect it is clothed with long dark coarse close pubescence; behind this the sternite displays a smooth shining unpunctured area broadening out posteriorly. *Legs* black. Anterior tibiae strongly broadened from base to apex where they are about two-fifths as broad as long; outer edge almost smooth in the basal half, then with a small prominent tooth separated by three equal extremely small teeth from a similar more prominent tooth at the apical angle, beyond this a tooth of similar size intervenes before the narrow subtarsal plate. Intermediate tibiae not strongly broadened, widest in the middle, outer edge evenly rounded and furnished with close short spines. Hind tibiae widest at the apical fourth, with inner edge feebly convex, outer edge set with close spines, longer and finer than those of the intermediate pair. Front tarsi strongly dilated, one and a third times as wide as the antennal club; intermediate tarsi slightly wider than, hind as wide as, the first antennal segment; last segment of all tarsi slightly shorter than the first four together; claws simple. *Genitalia* as figured (figs. 13 and 14). Tegmen large, with the apical excision U-shaped, its sides slightly divergent, not very deep, and with the lateral lobes not very long and broadly rounded at the apex.

Female.—Differs from the male in the following external characters: the anterior tibiae are less strongly dilated, being parallel-sided in the apical half, and at the apex one third as wide as long; front tarsi not dilated, one and a half times as wide as the first antennal segment; intermediate and hind tarsi as wide as this segment; the metasternum is simple, lacking the secondary sexual characters of the male; the last sternite is similarly simple. Ovipositor as figured (fig. 22); deeply pigmented, sharply pointed, with the styli at a distance from the apex equal to their own length.

Type ♂, FRENCH MOROCCO: Oued Zat, in a flower of *Convolvulus arvensis* L., 9.iv.1952 (*A. M. Easton*). In the author's collection.

Paratypes.—In the collection of the Institut Scientifique Chérifien, FRENCH MOROCCO: Tagdempt, Oued Mina, 1 ex.; Aguelmane, Azigza, 1800 m. (*Panouse*), 1 ex.; Iknioun, 2000 m. (*Kocher*), 1 ex. previously determined as



FIGS. 15–22.—Ventral view of ovipositors. (15) *Meligethes acicularis* Brisout. (16) *M. submetallicus* Deville. (17) *M. mikado* Reitter. (18) *M. normandi* sp. n. (19) *M. lugubris* Sturm. (20) *M. gagathinus* Erichson. (21) *M. egenus* Erichson. (22) *M. otini* sp. n. Scale D = 0·25 mm.

villosus Brisout; Forêt de la Mamora (*Kocher*), 2 ex. previously regarded as *planiusculus* Heer; el Hajeb, 1200 m., 1 ex. and Volubilis, 400 m., 1 ex., both previously considered to be *lugubris* Sturm. In the collection of M. Henri Otin of Meknès, Morocco: Fès, 2.vi.41, 1 ex.; Sefrou, 4.viii.40, 1 ex.

Variations.—Amongst the paratypes length varies from 2·05 to 2·3 mm. The degree of reticulation of the surface of the elytra is variable but much depends on the direction of the light by which it is examined, it is always most marked towards the apex, and never as distinct as in the closely related *M. egenus* Erichson. The denticulation of the outer edge of the front tibiae is very constant in form, but the number of small teeth between the two more prominent ones varies from two to four. The sides of the apical excision of the tegmen are at times more divergent than in the type specimen.

Comparative notes.—Very nearly related to *M. egenus* Erichson, *M. otini*, like that species, is distinguished from others of its Western and South African relatives by the microscopical reticulation of the upper surface of its elytra. It differs from them also, as from the Eastern *nitidicollis* Reitter and *mikado* Reitter, in its specific male secondary sexual characters, and in the form of its aedeagus. Its distinction from *M. egenus* may be tabulated as follows.

M. otini sp. n.	*M. egenus* Erichson.
More shining.	Less shining.
Legs very slightly narrower.	Legs very slightly broader.
Surface of pronotum between the punctures, except sometimes at the extreme base, smooth, non-reticulate.	Surface of the pronotum very variable, sometimes distinctly reticulate throughout, sometimes smooth except at the extreme base.
Surface of elytra between the punctures much less distinctly reticulate, sometimes very indistinctly so.	Surface of the elytra between the punctures always distinctly microscopically reticulate, hence duller.
Edge of metasternum close to hind trochanters very feebly raised in the male, not at all in the female.	Edge of metasternum close to hind trochanters very strongly raised in the male, moderately strongly in the female.
Male metasternum with triangular depression occupying hind $\frac{2}{3}$ to $\frac{3}{5}$, so that the tubercle at its apex is well in front of the centre.	Male metasternum with triangular depression occupying hind half, so that the longitudinal ridge at its apex is centrally placed.
Last sternite of male with a central transverse raised ridge, on the posterior aspect of which is a tuft of dark pubescence, and behind this a smooth area distinctly less wide than the hind edge of the metasternum.	Last sternite of male with a central blunt tubercle, on the posterior aspect of which is a tuft of dark pubescence, and behind this a smooth area about as wide as the hind edge of the metasternum.
Tegmen of aedeagus with the apical excision U-shaped, so that its sides are subparallel, and less deep, but somewhat variable; lateral lobes shorter and with ends widely rounded.	Tegmen of aedeagus with the apical excision in the form of a V with its apex truncate, thus its sides are more divergent, and deeper; lateral lobes longer and more sharply pointed (but wearing from age renders the lateral lobes shorter and blunter, and the excision less deep).
Ovipositor more elongate, and with apex more acute and sharper.	Ovipositor less elongate, and with apex less acute.

Biological notes.—From my own experience this species is uncommon as early in the year as April. M. Otin's examples were taken in June and August, M. Kocher's in May, whilst the specimen from Tagdempt bears the cipher X, which presumably denotes the month of October. Be this as it may, it is clear that *M. otini* is exceptionally late in its appearance, a fact which indicates attachment to a late flowering plant. Obviously *Convolvulus arvensis* L. cannot function as the host of the species, and it appears to me as almost certain that this rôle is filled by *Mentha rotundifolia* L., a plant which is common in French Morocco and, like most of the mints, late flowering, and which, moreover, in Europe constitutes the host-plant of *M. egenus* Erichson.

SUMMARY.

The *lugubris* complex in the Nitidulid genus *Meligethes* is defined. An attempt is made to resolve the confusion which has existed amongst the very closely related species comprising it. This has resulted in some revision of nomenclature, and new synonymies have been cited. Two new species, both from North Africa, are described, and fuller descriptions given of two others which were hitherto imperfectly understood. A taxonomic key to the species is included, and the genitalia, so far as they are known, are described and figured. Brief notes are given summarising the present scant knowledge of the specific host-plants.

ADDENDUM.

Since this paper was written the author has received a large consignment of *Meligethes* collected in Afghanistan. These include, in some numbers, two additional new species of the *lugubris* complex. As it is now too late to include these in the present revision, their descriptions will be given at a later date in a paper dealing with the Afghanistan *Meligethes* as a whole.

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THE *PARAGUS SERRATUS* COMPLEX, WITH DESCRIPTIONS OF NEW SPECIES (DIPTERA: SYRPHIDAE).*

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Manuscript received 26th October, 1953.
(Read 6th May, 1954.)

With 33 Text-figures.

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1. Introduction.

Paragus serratus was described, as a species of *Mulio*, by Fabricius in 1805 on material from India. At that time it was quite distinct from other species of *Paragus* because of its strongly serrated scutellum and carinate abdomen. A closely related species, *crenulatus*, was then described by Thomson (1868) on material from China. Later workers found that *P. serratus* was widely distributed. Verrall (1898) recorded that Lt.-Col. Yerbury had taken it at Aden—he also observed that Yerbury had found the species to be very common in Ceylon. Ricardo (1903) found a male and female in the collection made on Sokotra by W. R. O. Grant. Brunetti (1908) observed that it was common in India. The first record of *P. serratus* in Africa is that of Speiser (1911), who obtained specimens from Eritrea. Bezzi (1912) found *P. serratus* in the Fea collection from Portuguese Guinea—he remarked that he had seen specimens from Central Africa and Mozambique in the British Museum, and he commented briefly on a variable form of the species from the Cape Verde Islands—he observed that the species extended from Ceylon to New Guinea and appeared to have originated in the East. Bezzi compared African specimens with some from India and concluded that they were the same species. Specimens of *P. serratus* were then recorded from the Belgian Congo by Hervé-

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* Thesis submitted in partial fulfilment of the requirements for the degree of Master of Science of Rhodes University.

Bazin (1914), who stated that his record served to show how large the area of distribution of the species was. Bezzi (1915) found specimens in the British Museum collection from Mozambique, Durban, Sierra Leone and Nyasaland. He remarked that *P. serratus* was widely distributed south of the Sahara. Additional records of its distribution in Africa are those of Bezzi (1920), Efflatoun Bey (1926) and Curran (1938), who recorded specimens from Abyssinia, Egypt and Lourenço Marques respectively. It has also been found in Australia (Hardy, 1933). Recently Hull (1949) described a third species, *azurea*, on the female taken in Sokotra by Grant in 1899. Thus three closely related species, *P. serratus*, *crenulatus* and *azurea*, all quite distinct from other species of the genus, have been described. Of these, *P. azurea* has been recorded only from Sokotra, and *crenulatus* is known only from China, while *serratus* has been recorded from most of Africa south of the Sahara, Egypt, Aden, India, Ceylon, Java, New Guinea and even Australia.

When I commenced a revision of the African species of *Paragus* I was at once struck by the extreme variation found in coloration and size of individuals of *P. serratus*. This variation has often been commented on before (Verrall, 1898; Brunetti, 1908; de Meijere, 1908; Bezzi, 1912). I examined the male genitalia of several different colour forms taken in the same locality (Sawmills, Southern Rhodesia), and found that there were distinct, constant differences in structure which could be correlated with constant external features. After further study it became evident that the African forms could, on the material at my disposal, be divided into four distinct species, one of which was *P. azurea* Hull, on the basis of both external and genitalic characters. It then became necessary to determine the status of these species in relation to *P. serratus* as described by Fabricius.

The locality from which Fabricius obtained his material was Tranquebar, a town on the sea-coast in the Tanjore district of Madras, India (not Aden, as stated by Efflatoun Bey (1926)). An examination of Indian material became essential. A fine collection of *P. serratus s. lat.* from the Oriental Region, including specimens from the collections of Brunetti and Yerbury, was placed at my disposal by the British Museum. A study of this material has made it clear that there are four distinct Oriental species, *crenulatus*, *serratus*, and two new species, one of which also occurs in Africa. Thus the original *serratus* of Fabricius has been resolved into a complex of seven species, three of which are African, three Oriental, and one which is common to both regions. *P. serratus s. str.* is apparently confined to India.

2. Systematic Position of the *Paragus serratus* Complex.

The seven species forming the *serratus* complex belong to that section of the genus *Paragus* which has, amongst others, the following characteristics:
(1) The first five abdominal segments more or less rigidly fused together.
(2) The hair on the eyes usually arranged in vertical stripes.
(3) The compound eyes contiguous for some distance in the male.
(4) The spurious vein always ending at or before the point of coincidence of the fourth longitudinal vein and the lower marginal cross-vein.
(5) The inferior claspers of the same size or better developed than the superior claspers.
(6) The second abdominal segment wider than the first segment.

The subdivision outlined above includes the more robust species which frequently have a red, brown or yellow coloration developed on the abdomen, and sometimes have the apical half of the scutellum yellow. The *serratus* complex is isolated within this group by the following features :

(1) The scutellum is very deeply serrated, bearing on its outer margin a row of conspicuous, peg-like teeth. A slightly serrated condition is found in many other species of *Paragus*, but the serrations are usually weak and inconspicuous.
(2) The third and fourth abdominal segments are carinate.
(3) The second abdominal segment is longitudinally narrower over the middle than the first segment. In other species of the group the second segment is usually considerably longer than the first.
(4) There is a distinct, elevated, transverse ridge across the middle of the anterior half of the first abdominal segment.
(5) The ventral surface of the scutellum is covered by a dense, white pubescence in all species of the *serratus* complex. This pubescence is absent in most other species of the group, but is present, though sparse and very short, in a few undetermined species.
(6) There are two well developed longitudinal strips of tomentum on the mesonotum—the two inner ends of the transverse suture are filled with linear strips of tomentum.
(7) There is a facial stripe in the male—it is not always well developed and is often abbreviated, but seems to occur, except for the *tibialis* group, only within the *serratus* complex.
(8) The penis-sheath is developed on each side into a prominent process for the support of the superior claspers, and is usually produced below into a median, finger-like process.

3. Specific Characters.

In each description only those characters which I have found to show the greatest interspecific variation have been used. These may be listed as follows :

Head.—The colour of the face and slightly elevated strip of the epistome surrounding the oral tubercle ; the extent and colour of the facial stripe ; the nature of the facial pile ; the colour and relative lengths of the antennal segments ; the length of the antennae in relation to the distance between their base and the upper margin of the oral tubercle ; the colour of the vertex ; the nature of the stripes of hair on the eyes ; in the females, the colour of the frons and nature of the tomentose strips bordering it.

Thorax.—The colour of the reflections of the mesonotum ; the degree of puncturation ; the nature of the mesonotal pile and tomentose strips ; the coloration of the scutellum and nature of its teeth. The coloration of the legs, especially of the posterior femora. The colour and thickness of the wing veins ; the colour of the stigma ; the presence or absence of suffusion of the membrane.

Abdomen.—The shape and size of the abdomen ; its coloration ; the nature of the three pairs of tomentose vittae found on the posterior three segments ; the nature of the transverse troughs on segments three and four, which are occupied by the two anterior pairs of vittae; the nature of the vestiture of the abdomen; the degree of development and distribution of a honeycomb-like sculpturation on the tergites of the abdomen. The segmentation of the abdomen and some of the features mentioned above are indicated in fig. 1. Outline drawings of the abdomens of males and females of each species are given, all drawn to the same scale.

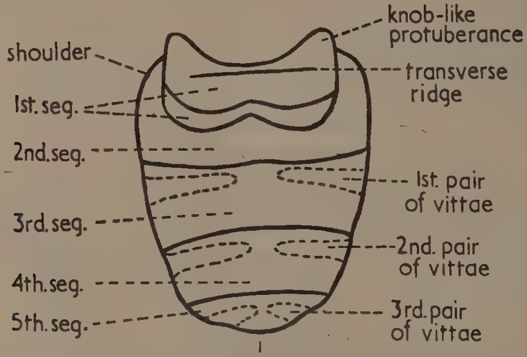

knob-like protuberance
shoulder
transverse ridge
Ist. seg.
2nd. seg.
Ist. pair of vittae
3rd. seg.
2nd. pair of vittae
4th. seg.
5th. seg.
3rd. pair of vittae
1

FIG. 1.—Diagram of abdomen, illustrating those features referred to in descriptions of the species.

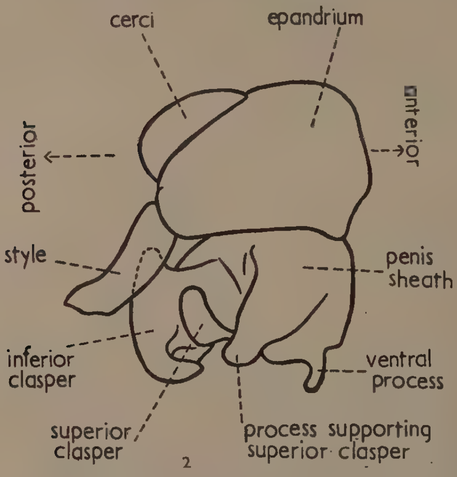

cerci
epandrium
posterior
anterior
style
penis sheath
inferior clasper
ventral process
superior clasper
process supporting superior clasper
2

FIG. 2.—Diagram of hypopygium, illustrating those features referred to in descriptions of the species.

Male genitalia.—Studies of the male genitalia have proved to be of the greatest use in separating the species. It is unfortunate that systematists have ignored them in the past when dealing with species of *Paragus*. In describing the genitalia I have used Metcalf's (1921) terminology, which is based on that of Wesche (1906). I have followed Zumpt and Heinz (1949) in calling the large, trough-shaped sclerite which bears the cerci and styles the " epandrium " and not " tergite ten " as Metcalf did. In numbering the segments of the abdomen I have counted the first apparent segment as being number one. All orientations mentioned in the text refer to the original, non-inverted condition of the hypopygium. Unless otherwise stated, the genitalia have been described as seen in lateral view. The different structures which have been of greatest use in separating the species are indicated in fig. 2.

4. Key to the African Species.

1 (2). Abdomen with conspicuous reclinate black hairs ; pile of mesonotum distinctly golden-yellow . . . . **auritus** sp. n.

2 (1). Black hairs of abdomen inconspicuous ; mesonotal pile white or pale yellow.

3 (6). Pile of mesonotum short ; antennae with the third segment not more than twice as long as the first two together ; the abdomen of the female is narrow when a small, diagonal spot of pollen is present on each side of the anterior ocellus.

4 (5). Abdomen narrow, melanic, with a patch of much lighter colour over the second and third segments ; thorax with cyanescent reflections ; female with a small, diagonal spot of pollen on each side of the anterior ocellus, and with the fourth and fifth abdominal sternites blackish . . . . **pusillus** sp. n.

5 (4). Abdomen broad, uniformly red-brown except for the shoulders which are piceous, sometimes the fourth segment is a little dark, rarely the whole abdomen black, never with a distinct patch of lighter colour over the second and third segments ; thorax dull, rarely with a few blue reflections, and quite heavily punctate ; female without a spot of pollen on each side of the anterior ocellus, and with the fourth and fifth abdominal sternites fuscous **capricorni** sp. n.

6 (3). Pile of mesonotum long ; antennae with the third segment more than twice as long as the first two together ; the abdomen of the female is stout when a spot of pollen is present on each side of the anterior ocellus.

7 (8). Mesonotal stripes abbreviated in the male, absent in the female ; sculpturation of the abdomen very reduced ; thorax with strong metallic blue reflections ; female without a small spot of pollen on each side of the anterior ocellus ; Sokotra . . . **azurea** Hull

8 (7). Mesonotal stripes complete in the male, complete though narrowed at the posterior ends in the female ; sculpturation of abdomen well developed ; thorax without very strong reflections ; female with a small, diagonal spot of pollen on each side of the anterior ocellus . . . . **azurea** subsp. **scrupeus** subsp. n.

5. Key to the Oriental Species.

1 (2). A transverse band of black across nearly the whole of the first abdominal segment in both sexes ; abdomen of male (figs. 27, 28) truncated, each posterior corner prominent, protruding and rounded ; the female with very deep, narrow, transverse troughs on the third and fourth abdominal segments . **yerburiensis** sp. n.

2 (1). Neither sex with a transverse band of black across most of the first abdominal segment; abdomen of male not truncated, without prominent posterior corners; the female without very deep and narrow troughs on the third and fourth abdominal segments.

3 (4). Large species (7·3–9·0 mm.); antennae longer than the distance between their base and the upper margin of the oral tubercle; posterior femora with very little or no dark brown; abdomen of females greatly distended . . . . **auritus** sp. n.

4 (3). Smaller species (5·1–6·8 mm.); antennae as long as the distance between their base and the upper margin of the oral tubercle; posterior femora banded with dark brown; abdomen of female normal.

5 (6). Wings usually suffused with yellow-brown; posterior femora almost entirely dark brown; mesonotal pile longish; many conspicuous, reclinate, black hairs on the abdomen **crenulatus** Thomson

6 (5). Wings hyaline, never suffused with yellow-brown; posterior femora with a narrow band of darkish brown; mesonotal pile short; black hairs on the abdomen sparse and very inconspicuous **serratus** (Fabricius)

6. Key to the African Species Based on Genitalic Characters.

1 (4). Penis sheath with a prominent, median, ventral process.

2 (3). Styles foliaceous, ending in points; epandrium not very elongated; superior claspers borne on rounded lobes; ejaculatory apodeme much smaller than the hypopygium (figs. 7–8) . . . **pusillus** sp. n.

3 (2). Styles with subparallel margins, not ending in points, but bluntly rounded; epandrium elongated; superior claspers borne on small, pointed processes; ejaculatory apodeme as large as the hypopygium (figs. 3–4) . . . . **capricorni** sp. n.

4 (1). Penis sheath completely lacking a median ventral process.

5 (6). Superior claspers borne on long, narrow, protruding processes; epandrium without a swelling on each side near the anterior corners (figs. 30–31) . . . . **auritus** sp. n.

6 (5). Superior claspers borne on moderately broad, bluntly rounded processes; epandrium with a swelling on each side near the posterior corners (fig. 13) . . . . **azurea** Hull

7. Key to the Oriental Species Based on Genitalic Characters.

1 (6). Penis sheath with a median, ventral process, which may sometimes be rather weak.

2 (3). Superior claspers borne on long, thin, pointed processes; inferior claspers enormously developed, as long as the epandrium, which is elongated (fig. 26) . . . . **yerburiensis** sp. n.

3 (2). Superior claspers borne on broad, rounded lobes; inferior claspers not enormously developed; epandrium not elongated.

4 (5). Styles distinctly narrowed in the middle (figs. 21–22) **serratus** (Fabricius).

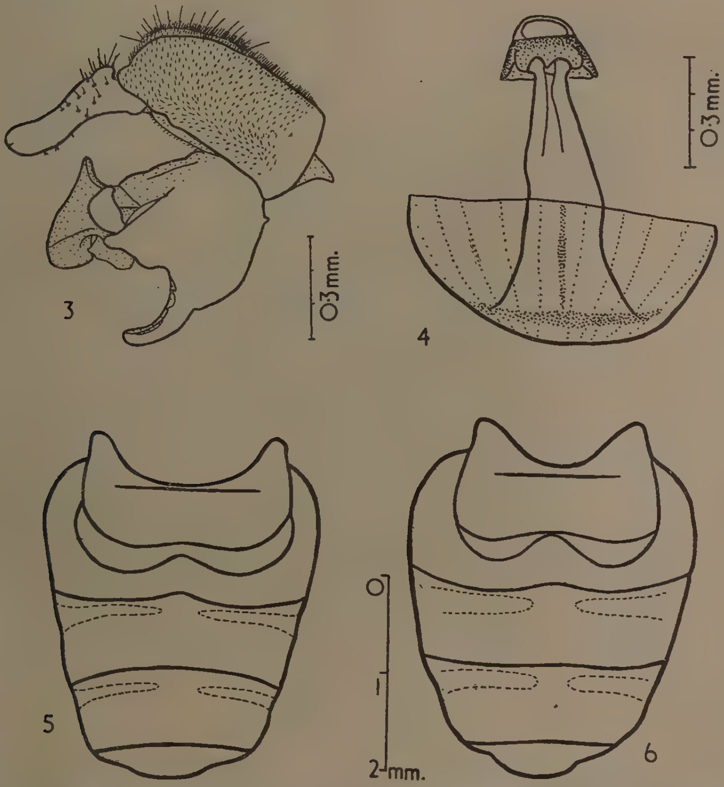
5 (4). Styles not narrowed in the middle (figs. 17–18) . . **crenulatus** Thomson.

6 (1). Penis sheath completely lacking a median, ventral process; superior claspers borne on long, narrow, protruding processes . **auritus** sp. n.

8. TAXONOMY.

Paragus capricorni sp. n.

A species with an almost entirely reddish-brown abdomen. The thorax is dull black, generally lacks coloured reflections, and is quite heavily punctate. The antennae are short, and the femora are reddish-brown without bands of darker colour. The epandrium is elongated, and there is a large, median, finger-like projection on the ventral surface of the penis sheath. The ejaculatory apodeme is very large.



FIGS. 3–6.—*Paragus capricorni* sp. n. (3) Hypopygium of holotype. (4) Ejaculatory apodeme. (5) Abdomen of holotype. (6) Abdomen of allotype.

Male.—Head : Face yellow, evenly covered with distinct punctures, and with a sparse silvery-white facial pile ; a narrow, median stripe present, extending from oral margin almost to base of antennae, conspicuously ligneous brown over the facial tubercle and almost colourless on its upper third. Oral tubercle piceous, and surrounded by a strip of dark brown. Two basal segments of antennae leather brown, the first slightly paler than the second ; third segment dull crineous, paler on its lower half, and twice as long as first two segments together. Vertex black, with pale violaceous reflections. Stripes of hair on eyes moderately distinct, and each outer stripe broadly interrupted in the middle. *Thorax*: Mesonotum dull black with colourless reflections, in some positions appearing to be the colour of pencil lead; irregularly and conspicuously punctate. Mesonotal pile short, erect and yellow. Dorsal stripes pale; just meeting at anterior margin of prescutum, and diverging posteriorly, each becoming narrower and ending almost in a point at posterior margin of scutum. Scutellum fuscous on basal half, slightly paler medially, and with apical half of the same yellow as the face. Fourteen yellowish-brown, prominent scutellar teeth present, each tipped with brown. Laterally the scutellum bears a few longish, silvery white hairs. *Legs:* All femora reddish-brown, almost dark amber, and translucent. Apical sixth of each femur and basal half of each tibia pale yellow. Tarsi ferruginous. *Wings:* Hyaline, with a glossy membrane. Stigma yellow, slightly tinged with brown; subcosta, humeral cross-vein, basal and apical parts of first longitudinal vein testaceous; remainder of veins very dark brown. *Abdomen* (fig. 5)*:* A distinctive reddish-brown, almost ferruginous, and a little dark on the apical segments; corners and knob-like protuberances of the first segment fusco-piceous. Third and fourth segments distinctly carinate, with somewhat flattened sides. Abdomen subtruncated apically, with abruptly rounded corners; its margins diverging, each curving only slightly, then curving rapidly into prominent shoulders; greatest width is across middle of first segment. The three pairs of white vittae distinct, and not meeting in the median line; transverse furrows on third and fourth segments narrow and moderately deep. Surface of second, third, fourth, and to a lesser extent the fifth, segments quite heavily sculptured, and with numerous small, inconspicuous, reclinate black hairs. First tergite smoother, but quite heavily punctate. Short, white hairs present on all segments, most noticeably on the fifth, where they are quite long; elsewhere they are reclinate, sparse and inconspicuous. *Genitalia* (fig. 3)*:* Epandrium elongate and rectangular, with its dorsal posterior corner broadly rounded; about twice as long as deep. Cerci inconspicuous. Seen dorsally the epandrium is as broad as long, with protuberances at each apical corner. Styles have almost parallel margins, with apex curved slightly forward and bluntly rounded; each style about as long as epandrium is deep. Inferior claspers moderately developed; drawn dorsally into projecting points, and ventrally flattened and truncated; a little shorter than the styles. Superior claspers borne on bluntly pointed processes of penis-sheath. Penis-sheath bears a ventral, median, finger-like projection that curves gently forward and which is about three-quarters as long as inferior claspers. Ejaculatory apodeme (fig. 4) very large, as large as hypopygium; shaped like an open umbrella, with a broad flattened handle that is abruptly narrowed at its end; the " umbrella " portion about as deep as one-half of the length of the handle, and ellipsoidal in shape—its greatest width approximately equal to the length of the handle.

Length 7·2 mm.

Holotype male. SOUTHERN RHODESIA: Sawmills, 26.xii.1919. In the National Museum of Southern Rhodesia, Bulawayo.

Female.—Vestiture better developed than in the holotype, the white hairs on the abdomen and the stripes on the eyes being more conspicuous. Front black with bluish reflections, and bordered by two strips of silvery-white tomentum which broaden at their upper ends. Mesonotum in some positions shows faint blue reflections. Thirteen scutellar teeth. Abdomen (fig. 6) darker, fourth segment entirely fusco-piceous behind median vittae; area between first two pairs of vittae blackish laterally with faint blue reflections, and reddish-brown in the centre; anterior corners of third segment and sides of second segment dark, also with faint blue reflections; shoulders pale; remainder of abdomen reddish-brown. Abdomen stouter, deeper and less obviously carinate than that of holotype, with tergites rounded in cross-section and margins more curved. Fourth sternite fusco-piceous and fifth reddish-brown suffused with black.

Length 7·2 mm.

Allotype female, Southern Rhodesia : Sabi River, iii.1939. In the collection of the Department of Agriculture of Southern Rhodesia, Salisbury, (no. 6626).

Paratypes : South-West Africa : Kaoko Otavi, iii.1926, 1 ♂ ; Ombombo, ii.1926, 1 ♀. In the South African Museum, Cape Town. Belgian Congo : Elisabethville, 5.iv.1912, 1 ♂ (*Dr. J. C. Bequaert*). In the Museé du Congo Belge, Tervuren, Belgium. Uganda : Karamoja Province, Lobwor Hills, Aremo, iv.1951, 1 ♂ (*T. H. E. Jackson*). In the Coryndon Museum, Nairobi. Southern Rhodesia : Sawmills, 1.iv.1923; 1 ♂; 25.xii.1925, 1 ♀; 27.xii.1920, 1 ♀. In the National Museum of Southern Rhodesia. Zululand : M'fongosi, iii.–iv.1935, 1 ♀, 2 ♂ (*W. E. Jones*). In the South African Museum, Cape Town. South Africa : Pretoria, 30.i.1915, 1 ♂; Barberton, 9.x.1919, 1 ♀; P. (Premier ?) Mine, 11.iv.1914, 1 ♀ (*H. K. Munro*). In the South African National Insect Collection, Department of Entomology, Pretoria. Komati Poort, xi.1918, 1 ♂ (*R. W. Tucker*). In the South African Museum.

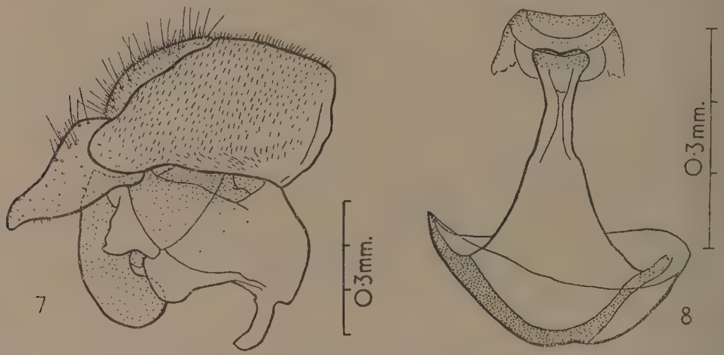
The male from Aremo, Uganda, is of exceptional interest as its abdomen is entirely dull black ; its antennae are almost black ; the sides of the mesonotum have green and cupreous reflections, the pile is brassy, the face is dusky yellow, and the median vitta is very dark and conspicuous. The specimen from Pretoria has amber legs and slight blue-green reflections on the thorax. The abdomen of the male from Elisabethville has a coloration like that of the allotype, except that the sides of the second segment are testaceous. The number of scutellar teeth varies from thirteen to fifteen. The genitalia of each male paratype have been examined and no variation has been noticed. The female from Premier Mine, South Africa, has a distinctly orange abdomen which is broader than that of the allotype and has the fourth and fifth sternites yellowish brown ; the legs are amber. Shortest paratype 5·4 mm., longest paratype 7·8 mm.

Remarks.—This species is easily distinguished from the other African species by the shape and colour of the abdomen. The females may resemble those of *P. azurea* subsp. *scrupeus*, but differ in that they lack the spots of pollen before the anterior ocellus. The name was suggested by the distribution of the specimens before me, which are grouped approximately across the Tropic of Capricorn. The male paratype from Elisabethville is the one mentioned by Hervé-Bazin (1914)—the female which he records is probably also of this species.

Paragus pusillus sp. n.

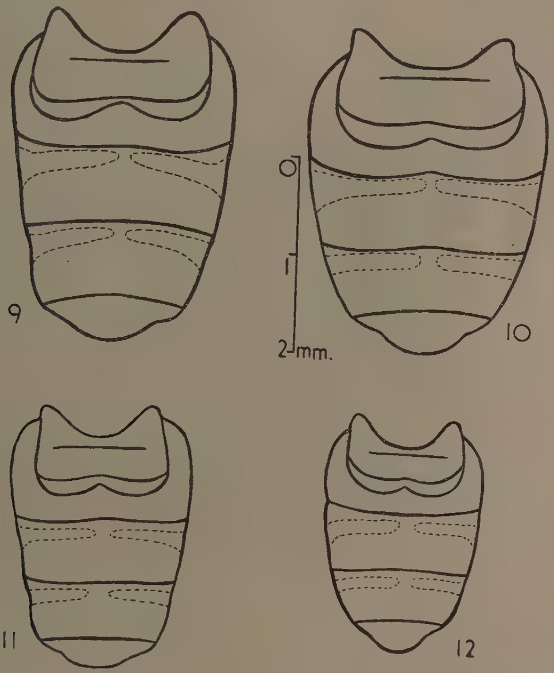
A narrow, dark species with very short mesonotal pile. The vertex of the male is closed behind by two posteriorly converging strips of tomentum. The femora are testaceous and lack bands of darker colour. The abdomen is very dark, except for a patch of lighter colour over the second and third segments. The females have a small, oval, diagonal spot of pollen on each side of the anterior ocellus. The styles are foliaceous and there is a prominent, median, finger-like process on the ventral surface of the penis-sheath. The ejaculatory apodeme is smaller than the hypopygium.

Male.—Head : Face creamy-yellow, with indistinct punctures and a sparse short silvery white pile ; facial stripe extends upwards to base of antennae, and is almost colourless except over the facial tubercle, where it is pale brown. Oral tubercle piceous and surrounded by a strip of light brown. Antennae shorter than the face; first segment badious; second similar, but dark above; third segment crineous, becoming brownish below, and twice as long as first two together. Vertex black with an admixture of brown, showing pale blue and cupreous reflections; bordered posteriorly by two small arms of silvery tomentum which converge at edge of occiput and extend anteriorly, ending at sides of vertex just past upper corners of compound eyes. Stripes of hair on eyes indistinct, the outer on each eye being almost absent and the inner two intermingling. *Thorax:* Mesonotum shining black with metallic blue and grey, and some slight cupreous reflections; conspicuously punctate. Mesonotal pile very short and scanty—it is bombycinous. Stripes on mesonotum moderately heavy, more so than in *P. capricorni*; converging anteriorly for a short distance, and not ending in sharp points posteriorly. Pile on posterior humeri slightly longer and paler. Scutellum creamy on apical third, colourless on middle third, and basally black with a strong admixture of brown. Fourteen long, yellow scutellar teeth. *Legs:* Femora testaceous basally, creamy-yellow on apical fifth. Posterior tibiae creamy-yellow basally, distally ferrugino-testaceous like the posterior tarsi. The two anterior pairs of tibiae creamy-yellow on basal half, testaceous distally. The two anterior pairs of tarsi testaceous, paler than femora. *Wings:* Hyaline, with a yellow stigma that is slightly tinged with brown. Apex of subcosta pale, almost the same colour as stigma. Remainder of veins ligneous brown, not as heavy as in *capricorni*. *Abdomen* (fig. 9): Very different from that of *P. capricorni*. Very dark, especially on first and last two segments. First segment almost entirely fusco-piceous except for a small, median, testaceous patch on its posterior margin. Second segment reddish in the centre, pale amber laterally, then slightly reddish-brown, the margins and shoulders fusco-piceous with pale blue reflections. Third segment dark reddish-brown with a darker median area, and becoming very dark on sides. Fourth segment entirely fusco-piceous, the fifth similar, except that it is margined with reddish-brown. Anterior vittae distinct, though not clearly defined against the pale colour of the second segment; middle and posterior pairs distinct, and each pair almost meets in the midline. Third and fourth segments distinctly carinate; their sides more rounded than in *P. capricorni*. Abdomen not robust, and narrow, with hardly prominent shoulders and margins nearly parallel; its apex rounded. Transverse troughs in which the vittae of third and fourth segments lie large and deep, especially the anterior pair. Tergites distinctly sculptured, including first segment; in addition there are numerous deep, round punctures evenly distributed over all tergites. A thin covering of short, very inconspicuous, reclinate black hairs, and longer, sparse, thin, white hairs present, erect on first segment and reclinate elsewhere.



Figs. 7–8.—*Paragus pusillus* sp. n. (7) Hypopygium of holotype. (8) Ejaculatory apodeme.

Genitalia (fig. 7): Epandrium rectangular, with posterior margin inclined at an angle to lower margin. Ratio of upper to lower margins 5 : 8. Epandrium about as deep as length of upper margin; its lower, posterior corner broadly rounded and produced. Cerci long, flattened and moderately prominent. Styles foliaceous when seen from the side, with upper and lower margins sinuate, upper more so than lower, both coming together at an acute angle and ending in a somewhat deflexed point. Inferior claspers well developed; extending ventrally into rounded lobes that project below level of penis sheath and bend cephalad a little; dorsally they are truncated at about level of lower margin of epandrium, with dorsal edge concave and meeting outer margin in a point; each about as long as epandrium is deep. Superior claspers borne on broad lobes with straightened edges.



FIGS. 9–12.—*Paragus pusillus* sp. n. (9) Abdomen of holotype. (10) Abdomen of allotype. (11) Abdomen of a small male. (12) A small female from South-West Africa.

Ventrally penis-sheath bears a finger-like projection that has a slightly concave inner surface, and which is about half as long as an inferior clasper. Ejaculatory apodeme missing in the preparation.

Length 6·2 mm.

Holotype male, SOUTHERN RHODESIA: Sawmills, 23.x.1922. In the National Museum of Southern Rhodesia, Bulawayo.

Female.—Facial stripe as broad as facial tubercle, and light ligneous brown. Tomentose strips on front linear and uniformly wide, and each with a short, beak-like, incurved hook of tomentum at upper end. Also a small, oval, diagonal spot of pollen on each side of anterior ocellus. Front black, with some metallic reflections. Stripes of hair on eyes distinct. Apical half of scutellum creamy-yellow; fourteen scutellar teeth. Abdomen like that of holotype, but darker; entirely piceous behind first pair of vittae and has a very dark fusiform patch in centre of second tergite. Abdomen (fig. 10) rounded in cross-section and slightly carinate, its shape similar to that of abdomen of holotype, but margins very gently curved from shoulders to apex. Fourth and fifth sternites shining black.

Length 6·4 mm.

Allotype female, SOUTH-WEST AFRICA: Zesfontein, ii.1925. In the South African Museum, Cape Town.

Paratypes: SOUTH-WEST AFRICA: Kaross, 1 ♂, 1 ♀; Zesfontein, 1 ♂, 2 ♀; Warmbad, 5 ♀, ii.1925. In the South African Museum, Cape Town.

The males are like the holotype, except that they are smaller and darker, the thorax of each specimen with only slightly coloured reflections. Each has only ten scutellar teeth and the yellow of the scutellum occupies the apical half. Their genitalia differ in having the styles with only slightly sinuate margins. The ejaculatory apodeme (fig. 8) from one paratype is very different from that of *P. capricorni*. It is much smaller than the hypopygium, and consists of a stem-like portion which bears a hood. The stem is very broadly flattened at its junction with the hood, expanding laterally into short, flattened flanges, and then tapering off quite slowly for a distance about equal to the greatest width of the hood—at this point it constricts slightly and then becomes cylindrical for a short length, finally dilating into a funnel-shaped apex. The hood is ellipsoidal, slightly distorted, and concave; dorsally it is furrowed over its greatest width along the line of attachment of the stem.

Of the female paratypes, two (Warmbad) are of the same size as the allotype, the rest smaller. They all have the coloured reflections of the thorax very poorly developed. The number of scutellar teeth varies from nine to fourteen. All appear to be almost completely black except for the lighter colouring on the second abdominal segment, and some have very reddish legs. Shortest paratype 4·6 mm., longest paratype 6·8 mm.

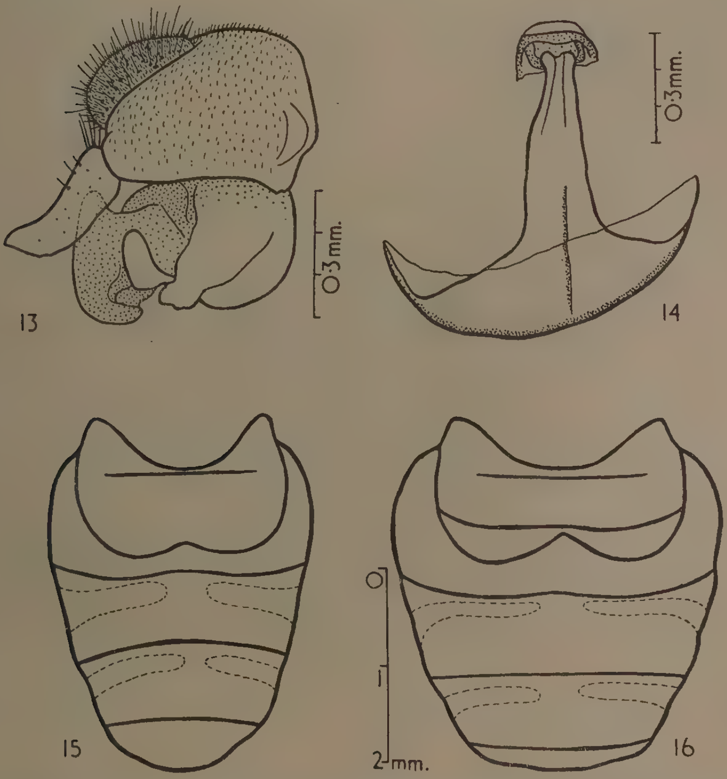
Remarks.—This species is distinguished by its small size, generally dark coloration and narrow body. It is easily separated from *P. capricorni* by the characters given in the key above, and from the other African species by its very short mesonotal pile. It appears to be most closely related to *P. serratus* (Fabricius). The dark coloration of the specimens from South-West Africa may be due to development under the semi-arid conditions usually prevailing there.

Paragus azurea Hull, 1949.

This species was established by Hull on a female taken in Sokotra by W. R. O. Grant. The male in the same collection was apparently overlooked, although its capture was recorded by Ricardo (1903 : 368), who also noted the bright metallic reflections of the thorax, the abbreviated condition of the mesonotal stripes in the male, and the absence of mesonotal stripes in the female. Grant added a note to the effect that the species was apparently scarce on the island.

A species with very long mesonotal pile and bright metallic reflections on the thorax. The mesonotal stripes are absent in the female, reduced in the male. The femora are banded with brown. The abdomen lacks sculpturation. There is a protuberance on each side of the epandrium near the lower, anterior corners.

Male.—Head : Face yellow, a little creamy, with a quite heavy, silvery white pile and a few small punctures. Facial stripe dark ligneous brown, its upper fifth thin and nearly colourless. Oral tubercle piceous, and surrounded by a strip of black which merges on each side with the black border of the oral margins. Basal segment of antennae brunneous ;



Figs. 13–16.—(13) Hypopygium of allotype of *Paragus azurea* Hull. (14) Ejaculatory apodeme of male of *scrupeus* subsp. n. from Mozambique. (15) Abdomen of allotype of *P. azurea*. (16) Abdomen of allotype of *scrupeus* subsp. n.

second segment the darkest, being fuscous dorsally and with a small spot of dark reddish-brown below ; third segment light crineous, darker dorsally, lighter on inner and ventral surfaces, rather elongated and cylindrical, and just over two-and-a-half times as long as first two segments together. Vertex fusco-piceous with pale violaceous reflections. Outer two stripes of hair on each eye distinct, inner stripe twice as broad as any of the others, and less sharply defined. *Thorax :* Mesonotum shining black with strong blue reflections, and a few violaceous reflections on the sides. A pair of pale, abbreviated dorsal stripes—these not meeting anteriorly and ending posteriorly just past the transverse suture. Mesonotal pile long, erect and white. Punctures on mesonotum small and widely separated. Basal third of scutellum fusco-piceous, the rest yellow; these two colours separated by a narrow, indefinite line of pale brown. Nineteen scutellar teeth of unequal length, those in the middle only half length of those on outside; each tipped with brown. *Legs:* Posterior femora dark brown in the centre; basal quarter dark testaceous and the apical fifth creamy-yellow. Posterior tibiae creamy for a little more than basal third, remainder tawny with a narrow, dark, median band. Posterior metatarsi fusco-testaceous but suffused with dark brown, the following segments similar but lighter, the last pale testaceous. Two anterior pairs of femora reddish-brown, with distal third creamy-yellow. Two anterior pairs of tibiae creamy-yellow for a little more than basal half, pale testaceous elsewhere. Two anterior pairs of tarsi pale testaceous. *Wings:* Hyaline, with a slightly clouded, yellow stigma. Subcosta yellowish-brown, its apex a little paler. Rest of veins ligneous brown, darker and a little heavier than in *P. pusillus* but not as dark or as heavy as in *capricorni*. *Abdomen* (fig. 15): Resembles that of *pusillus*. Sides and knob-like protuberances of first segment, and shoulders and margins of second segment all piceous with dull blue reflections: this dark colour proceeds more narrowly down entire margin of second segment to end at apical corners. Both first and second segments broadly translucent yellowish-brown over middle. Area between first two pairs of vittae irregularly dark reddish-brown and fuscous. Abdomen fusco-piceous behind the last pair of vittae except for an irregular reddish-brown, translucent patch which occupies about half of fifth segment and extends a little onto posterior part of fourth segment. Abdomen not carinate, angular, as if a little pinched, between vittae of third segment. Only a trace of a vitta on fifth segment; anterior vittae lie in shallow troughs that broaden very considerably laterally, and are somewhat indistinct against the pale colour of the second segment. Middle pair of vittae lie in very shallow and narrow troughs that do not widen laterally. Abdomen differs from that of *P. capricorni* and *pusillus* in the complete lack of sculpturation, tergites being smooth except for numerous deep, round, widely separated punctures. Short reclinate black hairs and some longer white hairs present on first segment, absent on the following two, and present on fifth segment and posterior margin of fourth. *Genitalia* (fig. 13): Epandrium rectangular, a little longer than deep; near the lower, anterior margin swollen into an anteriorly directed protuberance which is better developed on right side than on left. Cerci rounded and prominent. Styles flattened, with almost parallel margins, the upper margin sinuous, the lower slightly so; each style truncated apically and has upper distal corner produced. Inferior claspers moderately developed, rather ear-like with a slight ventral lobe, a somewhat pointed dorsal lobe, and a base nearly as broad as the whole. Superior claspers borne on broad lobes which have irregular margins. Penis-sheath broadly rounded below, with a slight transverse groove, and entirely lacking the finger-like projection found in *P. capricorni* and *pusillus*. Ejaculatory apodeme missing in the preparation.

Length 7·4 mm.

Allotype male, SOKOTRA: Hadibu Plains, 13.ii.1899, (*W. R. O. Grant*). In the British Museum (Natural History), B.M. 1916–75.

Remarks.—A very distinctive species on account of its long mesonotal pile, bright mesonotal reflections, and modified condition of the mesonotal stripes in both sexes. It is represented in Africa by the following subspecies, which seems to extend from Aden down the east coast as far south as Mozambique. The isolation of the typical form has probably accounted for its divergence from the continental stock.

Paragus azurea Hull, subsp. **scrupeus** subsp. n.

This subspecies differs from the typical form in having well developed sculpturation on the abdomen. The mesonotal stripes are complete in the male, almost complete in the female. The mesonotal pile is a little shorter, and the coloured reflections of the thorax are not as bright. The female has a small, diagonal spot of pollen on each side of the anterior ocellus.

Male.—Head : Face a darker yellow, with oral tubercle piceous but surrounded by a fusco-piceous band. Antennae differ in that second segment is only slightly dark above, and third segment is yellowish-brown on its lower half. Stripes of hair on eyes all of equal width. *Thorax :* Mesonotum a duller black, with some blue and violaceous reflections. Mesonotal pile shorter, but longer than that of *P. capricorni* and much longer than that of *pusillus* : it is bombycinous. Mesonotal stripes conspicuous and white, extending to base of scutellum—quite narrow and tapering only slightly, not ending in sharp points. Twelve subequal scutellar teeth, moderately long and each tipped with dark brown. *Legs :* Posterior femora less extensively brown, yellowish-testaceous on basal half, creamy-yellow on apical sixth and with a brown band between. Basal third of each posterior tibia creamy-yellow, tawny on remaining two-thirds. Posterior tarsi tawny. Two anterior pairs of femora yellowish-testaceous on basal two-thirds, a little lighter than on posterior pair, and creamy-yellow on the rest. The two pairs of remaining tibiae creamy yellow on basal half and, with their tarsi, the same colour as the femora elsewhere. *Wings :* Stigma pale, clear yellow, and veins light brown ; subcosta and apical part of first longitudinal vein yellowish-brown. *Abdomen :* Broader than in allotype of *P. azurea*, and shoulders more prominent ; sides flattened and triangular in cross-section, differing in this respect from *P. capricorni* and *pusillus* which have distinctly rounded sides. Third and fourth segments distinctly carinate. Sculpturation strongly developed on all segments. Transverse troughs on third segment not quite as deep or as wide. Abdomen brown, translucent, a little darker and reddish in places. Sides of second segment narrowly fusco-piceous, this dark colour continuing onto apical corners of first segment. *Genitalia :* Hypopygium similar to that of allotype of *P. azurea* described above, including presence of protuberances on each side of epandrium, but differs in some characters. Lower edge of epandrium a little arched, instead of being straight. Styles more produced apically, and almost straight below, but with a deeply sinuous upper margin. Base of penis-sheath with a distinct transverse furrow. Ejaculatory apodeme (fig. 14) larger than hypopygium, made up of two parts, an umbrella-like hood and a handle. The latter flat, expanded into wide lateral flanges along its basal attachment to the umbrella, slightly constricted apically and ending in a rounded knob. Umbrella ellipsoidal and concave, with a furrow along line of attachment to the handle, only half as deep as that of *P. capricorni*.

Length 7·2 mm.

Holotype male, ARABIA : Aden, 28.ii.1895 (*Lt.-Col. C. G. Nurse*). In the the British Museum (Natural History), B.M. 1934–8.

Female.—The single female before me differs from the holotype of *P. azurea* in many features. Lower half of frons reddish-brown, lighter just above base of antennae—this light patch bordered on each side by a strip of tomentum which widens dorsally and which is enlarged inwards at the upper end, the enlargement of each side not touching the other but separated narrowly. Dorsal part of frons bluish-black. On each side of anterior ocellus a small, oval, diagonal spot of pollen. Thorax black, with cyanescent and violaceous reflections. Mesonotal pile moderately long. Mesonotal stripes silvery-grey, just meeting anteriorly, and narrowing very abruptly posteriorly midway between transverse suture and scutellum, continuing to margin of scutellum as faint, broken, greyish lines. Posterior femora translucent and testaceous except for apical seventh, which is pale yellow. Wing veins light brown and thin. Scutellum fusco-piceous with a strong admixture of brown on basal half, yellow on the rest. Fourteen scutellar teeth which are conspicuously tipped with red-brown. Abdomen (fig. 6) very strongly carinate, deep and bowl-like—very broad and enlarged. Sides curve strongly backwards from prominent shoulders. Whole abdomen, including shoulders, dark red-brown—some fusco-piceous patches present on most of the segments, apparently due to consolidation of the contents of the abdomen and their adherence to the tergites. A well developed sculpturation on posterior four segments—the first segment coarsely punctate. Transverse troughs on third segment narrow and quite deep, and outer end of each curves backwards. Troughs on fourth segment likewise narrow and quite deep, but linear. Vittae white and prominent. Fourth and fifth sternites brown, irregularly marked with black.

Length 7·2 mm.

Allotype female, SOUTHERN RHODESIA: Sawmills, 25.xii.1925. In the National Museum of Southern Rhodesia, Bulawayo.

Paratypes: ARABIA: Aden, 5.iii.1895, 1 ♂ (*Lt.-Col. C. G. Nurse*). In the British Museum (Natural History), B.M. 1934–8. ZANZIBAR: nr. Mazi Moja, 20.viii.1924, 4 ♂ (*H. J. Snell*). In the British Museum (Natural History). PORTUGUESE EAST AFRICA: Masiene, xii.1924, 1 ♂ (*R. F. Lawrence*). In the South African National Insect Collection, Department of Entomology, Pretoria. Delagoa Bay, Inhaca Island, 29.iv.1953, 2 ♂ (*E. Giddy*).

The male from Aden has very heavy, silvery-white mesonotal stripes. The specimens from Zanzibar have the thorax more intensely black, with very dark blue reflections; two of the specimens have a creamy-yellow face, the other two are typical but have a very dark and conspicuous facial stripe. There is considerable variation in the colour of the abdomen, one specimen from Zanzibar being entirely fusco-piceous behind the first pair of vittae and over most of the first segment; the same specimen has pale antennae, the third segment being yellowish-brown. The male from Masiene has a very broad abdomen, shorter than in the other specimens, and which is dark fusco-piceous on the sides of the first three segments and entirely so on the fourth and fifth segments, translucent reddish-brown elsewhere. The genitalia of each male paratype has been examined and all are similar to that of the allotype of *P. azurea*; in each case the lower edge of the epandrium is straight, the condition found in the holotype of *scrupeus* apparently being unusual. The number of scutellar teeth varies from eleven to fourteen. Shortest paratype 5·4 mm., longest paratype 7·8 mm.

Remarks.—Specimens from the more southern part of the range of this subspecies may possibly be confused with *P. capricorni* as they tend to be darker than those from the north and have slightly shorter mesonotal pile. The males may be distinguished by the genitalia and by the longer antennae, while the females have a spot of pollen on each side of the anterior ocellus. The nine specimens taken at Aden by Yerbury (Verrall: 1898) probably belong to this subspecies. The specimens from Eritrea determined by Speiser (1911) as *P. serratus* almost certainly belong here, probably also the specimens from Egypt referred to by Efflatoun Bey (1926), and those from Lourenço Marques recorded by Curran (1938).

Paragus crenulatus Thomson, 1868.

This species was erected by Thomson on material from unspecified localities in China. From his description it would seem to differ from *P. serratus* as then understood in having extensively dark femora, longish antennae, the mesonotal stripes narrowed behind, and the wings yellowish at the base.

I have specimens before me from the following localities: SARAWAK: foot of Mt. Dulit at Junction of rivers Tinjar and Lejok, 22.viii.1932, 11.x.1932, 3 ♂, 1 ♀ (*B. M. Hobby, A. W. Moore*), B.M. 1933–254. HONG KONG: Hong Kong Peak, 22–24.ix.1937, 1300–1600 ft.; University Grounds, 1–10.xii.1937, 2 ♂, 4 ♀ (*G. M. Herford*), B.M. 1938–426. JAVA: Pekalongan, iv.1907, 1 ♂, C. H. Curran Collection, Acc. 31144. DUTCH NEW GUINEA: Cyclops Mts., Sabron, 930 ft., iv.1936, 1 ♀ (*L. E. Cheesman*), B.M. 1936–271. CEYLON: Colombo, 14.vi.1891, 1 ♂ (*Lt.-Col. Yerbury*), B.M. 1892–192. CELEBES: Molino, 4000 ft., i.1936, 1 ♀ (*L. E. Cheesman*), B.M. 1936–271. INDIA: Calcutta, xi.1908, 1 ♂, 20.xii.1908, 2 ♂, ex coll. Brunetti, B.M. 1927–184. MALAYA: Serdang, 17.xii.1923, 1 ♀ (*G. H. Corbett, B. A. R. Gater*), B.M. 1924–436. Singapore, 23.v.1911, 1 ♀ (*R. Hamitsch*), B.M. 1936–173. Selangor, Kuala Lumpur, 12.xi.1924, 1 ♀ (*H. M. Pendlebury*), B.M. 1925–56. SIAM: Bangkok, 19.vi.1929, 1 ♂, 1 ♀ (*W. R. S. Ladell*), B.M. 1930–215. All except the male from Java are in the British Museum.

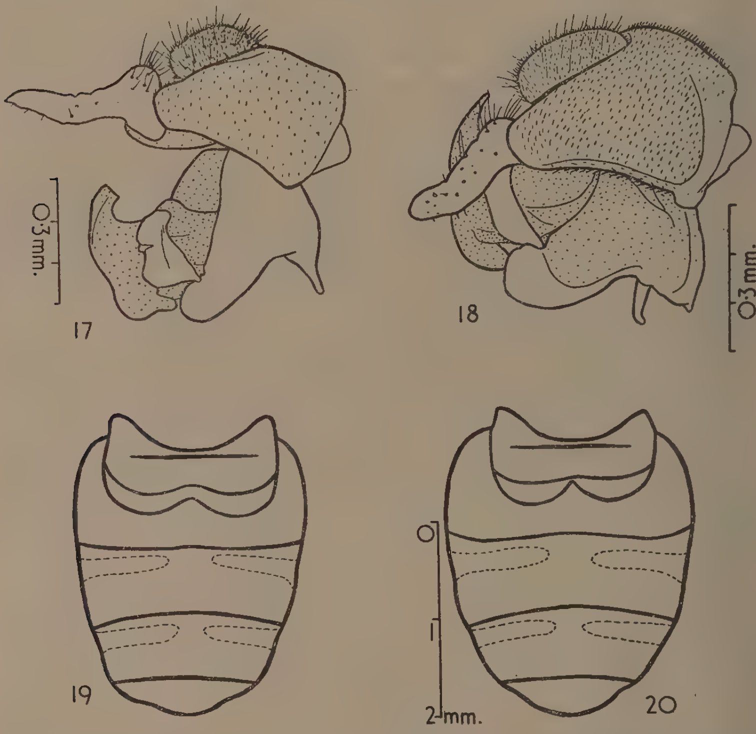
This is one of the most widely distributed species of the complex. It ranges over the whole of the Oriental Region and Austro-Malayan Subregion. The species which Keiser (1952) recorded from Sumba, Sumbawa, Flores and Timor as *P. serratus*, and which he notes to occur also in the Philippine Islands, Formosa and China, is almost certainly *P. crenulatus*. It is probably the species which occurs in Australia.

There is considerable variation within the species. Each of the larger islands has a slightly different form, and there are small differences between specimens from Malaya, Siam, India and Hong Kong. *P. crenulatus* could probably be divided into several subspecies; I lack sufficient material to attempt this.

The following description is based on the specimens from Hong Kong.

Males.—Head: Thomson states that the face of *P. crenulatus* is whitish—one of the males which I have has a flavescent face, translucent, and in some positions with very pale blue reflections; the other male has a yellow face.

Facial pile thin. Median stripe restricted in one specimen to the oral tubercle, in the other reaching half-way to antennae: pale brown in both. Oral tubercle conspicuously black, and surrounded by a dark brown strip. Two basal segments very dark brown, almost piceous above. Third segment paler, subcylindrical and a little more than twice as long as first two segments together. Vertex entirely black with violaceous reflections. The two middle stripes of hair on each eye tend to merge, but the outermost distinct though narrow. *Thorax:* Mesonotum black, with quite strong violaceous reflections and a few faint blue reflections. Mesonotal pile quite long, erect, and shining yellow: pale yellow on anterior humeri and shining brassy-yellow behind attachment of wings. Mesonotal stripes pale, rather purplish when seen from above—brassy-yellow when viewed obliquely. Stripes unite in front, almost uniformly wide as far back as midway between transverse suture and scutellum, and then narrow rapidly, almost ending in points. Basal third of scutellum piceous, the remainder yellowish. One male has eleven, the other twelve pale, subequal scutellar teeth (Thomson mentions twelve teeth). Scutellar pile decidedly longer than that of rest of mesonotum. *Legs:* Posterior femora testaceous on basal seventh, yellow on apical quarter, the rest conspicuously dark brown. Posterior tibiae yellow on basal half, then banded with dark brown, and with apical fifth tawny with a grey sheen. Posterior metatarsi dark crineous, rest of tarsal segments similar but more yellow. The two anterior pairs of femora yellow on apical half, luteous on basal half. The two anterior pairs of tibiae yellow on basal half, testaceous on the rest; the two anterior pairs of tarsi reddish-brown. *Wings :* Membrane suffused with yellowish-brown on the basal half, becoming paler apically. Microtrichia on membrane very dark and conspicuous, and the wing bordered posteriorly by a line which is darker than in the other species. Stigma yellowish-brown, distinctly darker than subcostal cell. Veins heavy and very dark, almost piceous. *Abdomen :* Broad and rather flattened, subcarinate. Over the second segment it is triangular in cross-section, less so over succeeding segments. Shoulders prominent, sides curving gradually backwards, forming sharply rounded corners behind. Shoulders dark fusco-piceous, with some violaceous reflections, this dark colour extending down the margin to apex of second segment, from whence it extends diagonally across the segment to posterior margin of first segment. Anterior corners and knob-like protuberances of first segment fusco-piceous. Remainder of abdomen brownish-amber, a little reddish behind. Prominent, reclinate, black hairs arising from distinct punctures on second, third, and, to a lesser extent, fourth segment. White hairs present on first segment, where they are thin and erect ; better developed and reclinate on fourth segment, and very well developed on fifth segment. Transverse troughs of third segment well developed, rather deep, with flattened sides. Troughs on fourth segment very shallow and inconspicuous. The vittae which normally occupy these troughs almost absent in



Figs. 17–20.—*Paragus crenulatus* Thomson. (17) Hypopygium of male from Hong Kong. (18) Hypopygium of male from Calcutta. (19) Abdomen of male from Java. (20) Abdomen of female from Hong Kong.

one specimen, sparingly developed in the other. Sculpturation present on second to fifth segments. *Genitalia* (fig. 17): Epandrium not very elongated, and its lower posterior corner bluntly rounded. Cerci rounded and prominent. Each style consists of an enlarged base and a narrow, elongated apical portion ending in a point and with sinuous upper and lower margins. Inferior claspers produced above into a moderately curved lobe which has a truncated end; ventrally they are produced into small, anteriorly directed lobes. Superior claspers borne on well developed, broadly rounded processes. A thin ventral projection present on penis-sheath.

Females.—Colour of face variable, being either flavescent, very smoky, translucent yellow, or almost yellow-green. Frons black with some bluish reflections bordered by narrow, linear strips of tomentum that expand at the upper end into a small, inwardly directed, triangular patch. Vertex black with violaceous reflections between ocelli and cyanescent reflections on the side and behind. Number of scutellar teeth varies from eleven to thirteen. Coloration of abdomen (fig. 20) considerably different from that of males described above, and practically the same in each female. First segment, including knob-like protuberances, black before the transverse ridge. Second segment wholly black on the sides, this dark colour extending diagonally across to posterior margin of first segment. Remainder of first and second segments, and narrow anterior margin of third segment brownish-amber. A small, black triangular patch in middle of second segment the arms of which in one specimen extend narrowly around entire posterior border of segment. Third segment completely fusco-piceous behind and between vittae. Fourth segment a little brownish before its vittae, remainder of segment black. Fifth segment dark brown, with irregular dark patches. All three pairs of vittae distinct and complete, though anterior margins of first pair are not clearly defined against the pale colour of anterior part of third segment. Abdomen almost uniformly broad as far back as beginning of third segment; very deep, incompletely carinate, and with slightly flattened sides. Fourth and fifth sternites dark fusco-piceous.

The specimens from Sarawak have yellow faces and prominent facial stripes. The antennae are paler, and the frons of the females and vertex of both sexes show strong cyanescent reflections. The thorax has violaceous and metallic cyanescent reflections. The mesonotal stripes, when seen from above, appear as two faint, purplish strips, scarcely discernible. When the thorax is viewed obliquely the stripes appear to be brassy or slightly cupreous; in all the specimens they fade out just behind the transverse suture. The number of scutellar teeth varies from twelve to fifteen. In two specimens the wings are only moderately suffused with yellow brown, otherwise they are heavily suffused. The genitalia differ in that the styles are more strongly arched on the upper margin, the epandrium is a little more elongated, and the processes supporting the superior claspers are not as well developed. Two of the males have the abdomen red-brown behind the first pair of vittae.

The female from Celebes has a darker face that is slightly tinged with brown. There are very strong cyanescent reflections on the front and vertex. The mesonotal pile is long, fine and bombycinous. The mesonotum is black and shining, with deep cyanescent reflections on the sides. The mesonotal stripes are complete though very thin over their posterior third, they are not very heavy, and are dark brassy yellow. The abdomen is greatly enlarged, almost as broad as long, and nearly circular in outline. The first segment is almost entirely yellowish-brown, except for a small dark patch below each knob-like protuberance. The area behind the vittae on the third segment is brownish medially, fusco-piceous on the sides. The fourth segment is fusco-piceous except for a narrow, median strip of dark brown. The anterior pair of vittae are inconspicuous, while the two posterior pairs are well developed. The troughs on the third and fourth segments are very shallow.

The female from Dutch New Guinea has a broad, rather flattened abdomen, with sides that curve strongly backwards. The third and fourth segments are conspicuously sculptured. The whole abdomen is a slightly reddish-brown, except for the sides and shoulders of the second segment which are piceous. The fourth and fifth sternites are yellowish-brown. The mesonotal pile is only faintly yellow, and the mesonotal stripes are silvery. The frons, vertex and entire mesonotum have deep cyanescent reflections. The tomentose strips of the vertex are linear and lack inward projections at the upper ends. The tarsi are rather ferruginous. There are eighteen scutellar teeth which are very short except for a few on each side of the scutellum.

The male from Java has very heavy mesonotal stripes which are silvery-white. The sides of the abdomen (fig. 19) are not so curved, and the abdomen is rather carinate. The knob-like protuberances of the first abdominal segment are fusco-piceous with quite strong blue reflections. The sides of the second segment are dark brown. The remainder of the abdomen is a slightly yellowish brown. The troughs on the third segment are narrow and quite deep. The hypopygium is very similar to that of the Hong Kong form, except that the penis-sheath is not so deeply curved below, and the ventral process is very weak.

The hypopygium of the male from Ceylon differs in certain respects from that of the Chinese specimens. The styles are not pointed apically, but bluntly rounded ; the upper lobe of the inferior claspers is more attenuated and almost ends in a point ; the process supporting the superior claspers is much broader.

The three specimens from Calcutta are rather dark. The abdomen is marked like those of the females from Hong Kong. The mesonotal pile is white, and the mesonotal stripes are complete and silvery. The wings in each case are without any suffusion. The thorax is more coarsely punctate, and has dull violaceous and a few cupreous reflections. The genitalia (fig. 18) differ in having the penis-sheath more broadly curved below, and the styles rounded apically and not enlarged at the base.

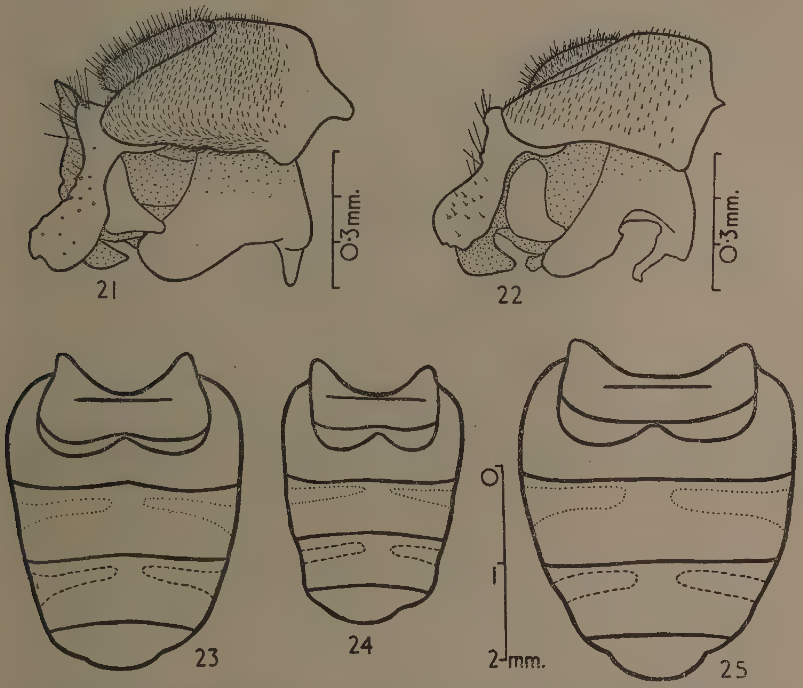
The male from Bangkok has no suffusion on the wings, and the veins are not as heavy as in the Chinese form. The thorax has some cyanescent reflections, and the mesonotal pile is pale yellow. The mesonotal stripes are complete and silvery. The abdomen is coloured like that of the male from Java. The epandrium is about as long as deep, the styles are enlarged at the base, and the upper lobe of the inferior claspers is more produced. The female from the same locality has moderately suffused wings, heavier mesonotal pile and a darkish face ; the tomentose strips of the frons are enlarged at the upper end into stout, hatchet-like projections that almost meet in the mid-line. The posterior femora of both specimens are only moderately dark.

Of the females from Malaya, those from Kuala Lumpur and Singapore have almost clear wings. All have the tomentose strips of the frons narrow, with stout, inwardly projecting, beak-like extensions at the upper ends, which almost meet in the mid-line. The specimen from Serdang has heavily suffused wings and has the fourth and fifth abdominal sternites brown. Shortest specimen 5·6 mm., longest specimen 6·8 mm.

Remarks.—This species can usually be recognised by its suffused wings, and by the extensively dark posterior femora. It may be confused with *P. serratus* (Fabricius) when the wings are clear, but the longer mesonotal pile and darker posterior femora distinguish it from that species. The shape of the abdomen is often characteristic.

Paragus serratus (Fabricius), 1805.

I have material from the localities given below: all the specimens are in the British Museum (Natural History). North-West India: Jubblepore, 24.ix.1907, 1 ♂ (*C. G. Nurse*), B.M. 1934–38; 15.xi.1907, 1 ♀, ex coll. Brunetti, B.M. 1927–184. Deesa, viii.1901, 1 ♂ (*C. G. Nurse*), B.M. 1934–38. North-East India: Delhi, x.1936, 1 ♂ (*T. Jermyn*), B.M. 1949–53. India: Poona, 19–27.ii.1907, 1 ♂, ex coll. Brunetti, B.M. 1927–184. Coimbatore, 13.viii.1912, 1 ♂ (R.S.V.). Hasi, 17.xi.1907, 1 ♀, ex coll. Brunetti, B.M. 1927-184. Mysore, Bangalore, 1 ♀ (*E. Y. Watson*).



Figs. 21–25.—*Paragus serratus* (Fabricius). (21) Hypopygium of male from Poona, India. (22) Hypopygium of male from Delhi, India. (23) Abdomen of male. (24) Abdomen of female.

Males.—Head: Face varies from sulphur-yellow to creamy-yellow. Facial stripe undeveloped except for a colourless or slightly brown patch over facial tubercle. Oral tubercle piceous, and surrounded by a narrow strip of slightly reddish-brown. Facial pile short and thin. Two basal segments of antennae dark red-brown, the second blackish above. Third segment pale crineous above, tawny on basal half, nearly twice as long as first two segments together, and moderately stout. Vertex fusco-piceous around ocelli, with some violaceous reflections; posteriorly it is black with metallic azureous reflections. Stripes of hair on eyes quite distinct, outer stripe on each eye narrowed in the middle. *Thorax:* Mesonotum black with strong violaceous reflections dorsally and strong blue reflections on the sides. Mesonotal pile short, pale, and golden-yellow. Mesonotal stripes heavy and broad, almost uniformly wide throughout their length, and not ending in sharp points; yellowish. Basal half of scutellum fusco-piceous, the remainder yellow. Scutellar teeth variable in length, those towards centre of row shortest, varying in number from ten to fourteen. *Legs:* All femora testaceous basally, creamy-yellow apically, a narrow, dark-brown band on posterior femora. Tibiae creamy-yellow on basal half, pale testaceous on the rest. Posterior tarsi ferrugino-testaceous, the two anterior pairs pale testaceous. *Wings:* Membrane hyaline and shining. Veins dark brown, and stigma a dirty yellow. *Abdomen* (figs. 23–24): Corners of first segment and shoulders and sides of second segment piceous, sometimes admixed with brown, and usually with bluish reflections. Remainder of first and second segments and anterior margin of third segment amber. Abdomen brown between anterior and posterior vittae, sometimes a little reddish, and rarely entirely amber. Moderately carinate on third and fourth segments. Anterior vittae indistinct and pale; posterior vittae moderately distinct and silvery-grey. Troughs on third segment wide and deep, sometimes rather narrow and moderately deep, those of fourth segment narrow and moderately deep. Sculpturation of fourth segment reduced; present, though inconspicuous, on second and third segments. Vestiture of abdomen poorly developed; middle three segments with many short, black, reclinate hairs, on first segment some short, thin, erect, white hairs, and on fourth segment a few similar hairs, only reclinate; some longer, silvery-white hairs on the fifth segment. *Genitalia* (figs. 21–22): Epandrium nearly one-and-a-half times as long as deep. Its anterior margin produced forwards on each side into triangular projections. Cerci flattish and quite prominent. Styles very characteristic, flat and wide apically, narrowly constricted over the middle, and dilated basally into a " head ". Inferior claspers well developed: ventrally produced into small, pointed, suboval lobes, dorsally they extend into long, laterally flattened lobes. Superior claspers borne on broad lobes. Penis-sheath very narrow ventrally, and bears a weak, short, median, ventral process.

Females.—The three females of this species before me are rather variable, and it is possible that the one from Hasi does not belong here.

Frons black with cyanescent reflections; in the female from Bangalore it is fusco-piceous like the vertex. Tomentose strips of the frons well developed, each broad and linear and inwardly expanded at upper end into stout, triangular patches, both almost meeting in the mid-line; the specimen from Hasi lacks these projections of the tomentose strips. Vertex fusco-piceous around the ocelli; cyanescent reflections posteriorly, except in the female from Bangalore. Number of scutellar teeth varies from fourteen to seventeen. Fourth and fifth abdominal sternites fusco-piceous, with a strong admixture of red-brown in places.

Longest specimen 6·8 mm., shortest specimen 5·1 mm.

Remarks.—The short mesonotal pile and male genitalia distinguish this species. The antennae are shortish, and the posterior femora are only narrowly dark.

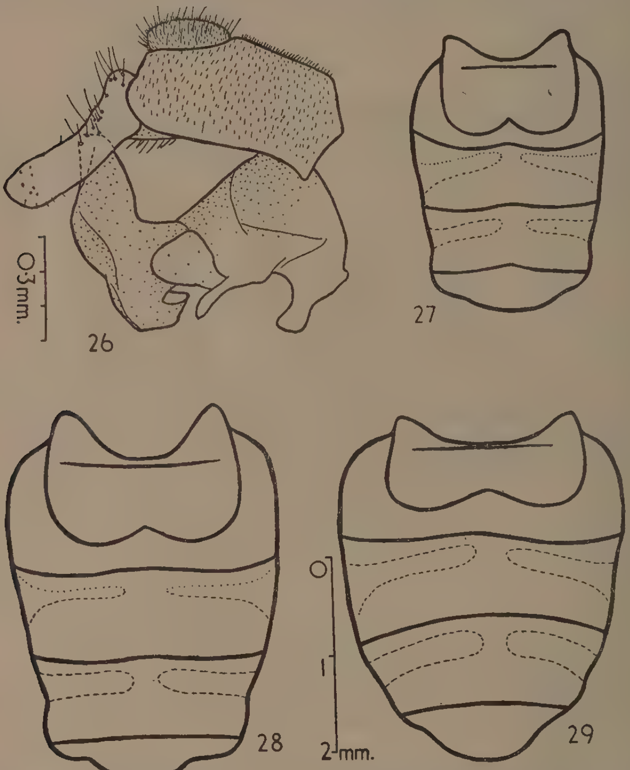
A translation of the original description of *P. serratus* is as follows, for which I am indebted to Mr. S. Whiteley: " With a black thorax, the edge of the scutellum yellow and serrate. It has the small stature of the preceding species (*P. bicolor*). Head yellow, antennae dusky; a black thorax with two shortened grey dorsal lines. Scutellum black, with extensive yellow on the rim, saw-like with many little teeth. Abdomen black on the first segment, red on the rest, with a whitish edge. Clear, unspotted wings; rust-red tarsi". The description is very brief, but I believe that it can be referred to the species described above for several reasons. It is unlikely that Fabricius described a specimen of *P. crenulatus* as he would have noticed the suffused wings; his type could not have been a specimen of *P. yerburiensis* as in that species the abdomen is not extensively reddish; finally, *P. auritus* is much larger than *bicolor*, and does not have rust-red tarsi. It seems probable that the species described above is *P. serratus* as it is the only Oriental species that agrees with his description on all points.

It is interesting to note that a Danish factory was opened at Tranquebar, the type locality, in 1620; Danish influence continued until 1845, except for a brief period of British Occupation from 1801 to 1814 (*Encyclopaedia Britannica*, 22, 14th edit., 1929). Fabricius probably came by his material of *P. serratus* through the efforts of these settlers. The species seems to be confined to India.

Paragus yerburiensis sp. n.

This species has a transverse band of black across most of the first abdominal segment. The posterior corners of the abdomen are very much produced, and the abdomen appears to be truncated in the males. The epandrium is elongated, the inferior claspers are greatly enlarged, and the superior claspers are borne on long narrow processes.

Male.—Head: Face dark yellow, with distinct punctures and a silvery-white pile. No median stripe, facial tubercle brown. Oral tubercle piceous, and surrounded by a dark brown strip. Two basal segments of antennae very dark brown, second segment suffused with black above. Third segment elongated and cylindrical, crineous above and tawny on lower surface at base, twice as long as first two together. Vertex fusco-piceous with dull violaceous reflections; tomentum of occiput extends for a short distance past upper corners of compound eyes, closing the vertex from behind. Stripes of hair on eyes distinct and quite heavy, outermost on each eye the widest, and broadly interrupted in the middle. *Thorax:* Mesonotum rather dull black, with pale violaceous reflections; quite heavily punctate. Mesonotal pile short and yellowish. Mesonotal stripes heavy and conspicuous, yellowish in front and grey behind, each broad, and meeting in region of transverse suture. Scutellum dark fusco-piceous on basal half, dark yellow on remainder. Sixteen long scutellar teeth, each tipped with black. *Legs:* Posterior femora with a very dark brown band on their median half, basal quarter testaceous, and apical quarter creamy-yellow. Posterior tibiae yellowish on basal half, ferrugino-testaceous with a dark median band on remainder. Whole tarsus missing from left posterior leg, and two apical segments missing on right leg, remaining three segments red-brown with a grey suffusion. The two anterior pairs of femora testaceous on basal two-thirds, pale yellow on the rest. The two anterior pairs of tibiae pale yellow on a little more than basal half, pale testaceous on remainder and on tarsi. *Wings:* Narrower than in the other species. Membrane hyaline and a little glossy. Stigma pale yellow, and veins very dark brown, almost black, and rather thin. Microtrichia on membrane sparse. Subcosta and apical part of first longitudinal vein brown. *Abdomen* (fig. 28): First segment piceous across more than its anterior half, this dark colour extending diagonally across each side of second segment, ending at apical corners of that segment. Second segment with a median, fusco-piceous, triangular patch. Third segment entirely fusco-piceous behind first pair of vittae, this colour extending forward between vittae, stopping at margin of second segment in alignment with the triangular patch mentioned above. Remainder of first three segments yellow-brown. Fourth segment fusco-piceous and fifth segment similar. Anterior margin of each anterior vitta inconspicuous against the paler colour of third segment, but posterior margin distinct against dark colour of that segment. Middle and posterior pairs of vittae distinct, and a little creamy. Abdomen of a characteristic shape. Sides almost parallel, diverging a little anteriorly, each curving gently backwards from moderately prominent shoulders. Second segment subtriangular in cross-section, third segment decidedly more rounded ; sides of posterior part of fourth segment vertical,



Figs. 26–29.—*Paragus yerburiensis* sp. n. (26) Hypopygium of holotype. (27) Abdomen of a small male. (28) Abdomen of holotype. (29) Abdomen of allotype.

a little curved above. Posterior corners of abdomen markedly produced and broadly rounded and swollen, giving the abdomen a rather truncated appearance. Margins of abdomen curve under these swellings. Troughs on fourth segment deep and narrow, those of third segment deep, but with shallow sides. Area between first two pairs of vittae strongly curved longitudinally as well as transversely. Abdomen a little carinate from between median to between anterior vittae. The dark part of first segment coarsely punctate, and with a thin covering of short white hairs which curve outwards from the median line on each side, remainder of segment impunctate. Triangular patch on second segment covered with large, close punctures which superficially resemble sculpturation, but out of which no hairs arise ; a few punctures and some sparse, reclinate, black hairs on remainder of segment. Towards anterior corners of third segment a few punctures out of which arise fine sparse, reclinate, white hairs, rest of the segment, behind the anterior vittae, lacks sculpturation. Some reduced punctures present, especially towards sides ; hairs lacking over median half but some reclinate black hairs present on sides. Fourth segment similar to third, but with very few punctures, appearing very smooth as a result ; some reclinate, black hairs on the sides. *Genitalia* (fig. 26) : Epandrium elongated and about twice as long as deep, its lower posterior corner broadly rounded. Cerci very prominent, and stand well above upper margin of epandrium. Styles about one-and-a-quarter times as long as epandrium is deep, quite broad and flattened, with subparallel margins, a bluntly pointed distal end and a slightly swollen base. Inferior claspers greatly enlarged and as long as epandrium is deep, dorsally produced into very long, flat, blade-like lobes which twist inwards a little at the tip. Ventrally they are produced into short, sharply truncated lobes which are broadened on inner surface into distinct, almost horizontal faces. Superior lobes borne on thin, sharply pointed processes. Lower surface of penis-sheath bears a median, ventral projection that is flattened laterally and subrectangular in shape.

Length 7·0 mm.

Holotype male, CEYLON : Velverry, 18.i.1891 (*Lt.-Col. Yerbury*). In the British Museum (Natural History), B.M. 1892–192.

Female.—Head with a black frons having blue-grey reflections. Strips of tomentum widened above, upper ends bending inwards, pointed and hook-like. Antennae stand on a dark brown base, their two basal segments very dark, and third segment darker than in holotype. Vertex black with strong cyanescent reflections. Scutellum yellow on a little more than apical third. Abdomen (fig. 29) coloured like that of holotype, with the following differences : triangular patch on second segment extended on both sides into thin, long curved arms which follow the border of first segment, and which are not quite complete, continuing apically as a series of about ten dark spots around some punctures ; dark areas on sides of second segment not extending diagonally across segment to end in its corners, but uniformly wide throughout, ending on posterior margin of second segment ; abdomen is piceous behind first pair of vittae. Shoulders prominent, and margins of abdomen parallel as far back as first pair of vittae. Troughs on third and fourth segments very deep, narrowish and distinct. Abdomen triangular in cross-section through second segment, more rounded through third segment, and much more rounded through fourth segment. A moderately developed sculpturation present on third and fourth segments. Fourth and fifth sternites black and shining.

Length 7·6 mm.

Allotype female, CEYLON : Mahagany, 30.xi.1890 (*Lt.-Col. Yerbury*). In the British Museum (Natural History), B.M. 1892–192.

Paratypes : INDIA : Jubblepore, 15.xi.1907, 1 ♂ ex coll. Brunetti, B.M. 1927–184. CEYLON : Mahagany, 30.xi.1890, 1 ♂ (*Lt.-Col. Yerbury*), B.M. 1892–192 ; Trincomali, 20.iii.1891, 1 ♂ (*Lt.-Col. Yerbury*), B.M. 1892–192.

The head of the paratype from Trincomali is missing. The dark colour of the antennae, especially of the two basal segments which are almost black, is a noticeable feature of the other two paratypes. All three specimens differ from the holotype in having the abdomen with a strong admixture of brown behind the first pair of vittae ; in the specimen from Trincomali this region is almost pure brown. They differ, too, in having distinct punctures on the third and fourth segments. There are some slight differences in the genitalia of each specimen, these involve the styles, which may be truncated or a little rounded apically, and which in all three paratypes have the upper margin a little sinuous.

Remarks.—This species is easily distinguished by the characters given in the key above. From the nature of the abdomen of the male and of the male genitalia it seems that *P. yerburiensis* is a rather isolated species within the complex. There seems to be considerable variation in size between individuals of this species.

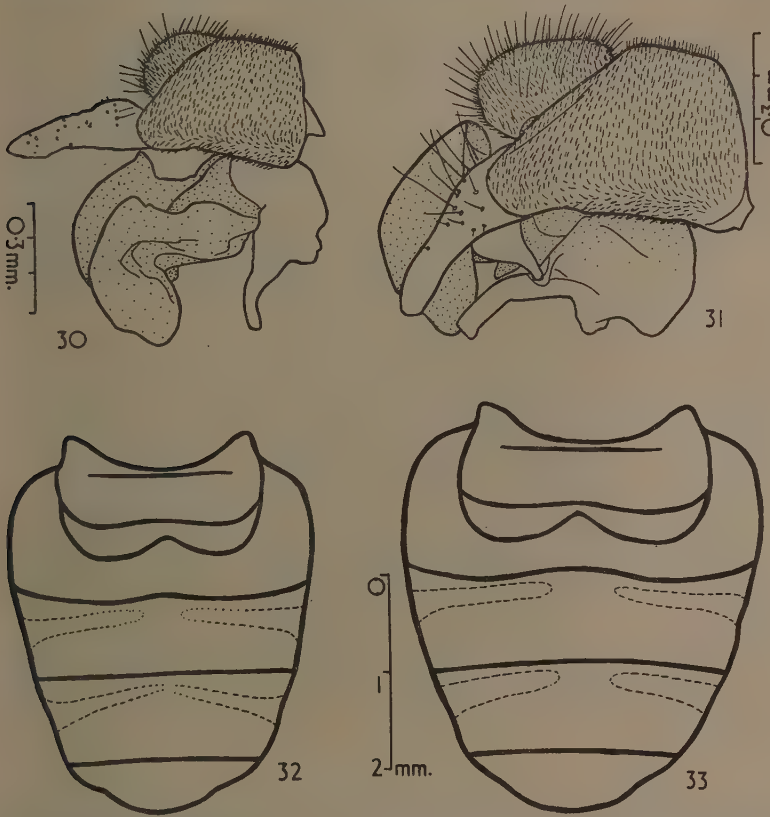
Paragus auritus sp. n.

This is a large species with elongated antennae. The abdomen is unusually broad in relation to the thorax, the females especially with greatly distended abdomens. There is no median, ventral projection on the penis-sheath, and the inferior claspers are produced into large ventral lobes. The superior claspers are borne on long, narrow processes.

Male.—Head : Face yellow, with small punctures and a short, moderately thick facial pile. Oral tubercle piceous and surrounded by a strip of light brown. Third segment of one antenna missing. Segments of other antenna very elongated, especially the third, and antenna as a whole longer than distance between base of antennae and upper margin of oral tubercle ; third segment tapering and cylindrical. Basal segments reddish-brown, the second darker than the first ; apical segment dark crineous above, somewhat orange below. Vertex black with strong violaceous reflections. Stripes of hair on eyes distinct, the outermost on each eye being the broadest. *Thorax :* Mesonotum black with pale blue and violet reflections above, and quite strong blue reflections on the sides, heavily punctate, the punctures rather small. Mesonotal pile quite short and thick, fine, erect and yellow. One of the mesonotal stripes has been obliterated by the pin on which the specimen is mounted, the other stripe distinct and quite heavy, yellow in front and silvery-grey behind. Scutellum fusco-piceous on basal half and slightly creamy-yellow on apical half : between these two areas a narrow intermediate band of brown. Sixteen scutellar teeth, each tipped with orange, the middle six teeth only half the length of those on the outside. *Legs :* Posterior femora brown on middle half, pale testaceous on basal quarter, and yellow on apical quarter. Posterior tibiae pale yellow, almost white on basal half, the remainder yellowish testaceous. Hind tarsi brown with a slight admixture of yellow. The two anterior pairs of femora pale testaceous, except for their distal fifth, which is yellow. The middle and anterior pairs of tibiae pale yellow on their basal two-thirds, very pale testaceous on remainder. The two anterior pairs of tarsi brown with a strong admixture of yellow, almost orange. *Wings :* Membrane hyaline and moderately glossy, slightly suffused on basal half. Stigma yellow and veins ligneous brown and moderately heavy. Subcosta and apical part of first longitudinal vein light brown. *Abdomen :* Conspicuously large in relation to thorax. Slightly carinate, rather rounded and deep, a little flattened on each side of median line, and with prominent shoulders ; translucent brown. Corners of first segment and shoulders of second suffused with dark brown, also fourth segment behind median vittae. A fine sculpturation present on fourth segment and that part of third segment behind anterior vittae. Remainder of abdomen covered with punctures. Middle three segments with a conspicuous covering of quite long, stout reclinate black hairs which are distinct against pale coloration of abdomen. White hairs present on fifth segment and also a few on fourth. Anterior vittae rather indistinct, and lying in shallow troughs ; middle and posterior vittae distinct, troughs on fourth segment shallow and narrow. *Genitalia* (fig. 30) : Epandrium trapezoid, with upper and lower sides parallel—not quite twice as long as deep. Ventral posterior corners broadly rounded. Cerci rounded and prominent. Styles shaped somewhat like the blade of a pen-knife, only with a broadened base and with upper and lower margins a little notched. Inferior claspers ear-like and well developed ; the upper lobe slight, but the lower lobe very large and produced ventrally. Penis sheath narrow, and completely lacking any median, ventral projection. Superior claspers borne on long, narrow, curved, ventrally-directed projections of the penis-sheath, these projections very characteristic.

Length 8·2 mm.

Holotype male, Ceylon : Kandy, 29.vi.1892 (*Lt.-Col. Yerbury*). In the British Museum (Natural History), B.M. 1892–192.



Figs. 30–33.—*Paragus auritus* sp. n. (30) Hypopygium of holotype. (31) Hypopygium of male from Kanthalia, Ceylon. (32) Abdomen of holotype. (33) Abdomen of allotype.

Female.—Third segment of antennae conspicuously darker than the two basal segments. Frons black with dull cyanescent reflections. The two tomentose strips broad and with irregular inner margins, each with a thin inward projection at upper end. Vertex fusco-piceous with violaceous reflections. Fifteen scutellar teeth. Wings quite strongly suffused with yellow-brown, more strongly so on basal half. Abdomen very broad and greatly enlarged in relation to thorax, very deep and rounded, with prominent shoulders. Sides curve rapidly backwards under the bulge of the abdomen (fig. 33). Fourth and fifth segments piceous except for a narrow strip of brown along anterior margin of each median vitta. Third segment with a fusco-piceous strip on each side of median line. Black hairs which were present on abdomen of holotype well developed and conspicuous, perhaps a little longer and thinner. Fourth and fifth sternites dark, shining fusco-piceous.

Length 8·2 mm.

Allotype female, CEYLON: Anarudhapura, 10.xii.1890 (*Lt.-Col. Yerbury*). In the British Museum (Natural History), B.M. 1892–192.

Paratypes: CEYLON: Kanthalia, 31.vii.1890, 17.x.1890, 2 ♂; Trincomali, 19.ii.1892, 1 ♀; Pankullam, 1.i.1891, 1 ♀ (*Lt.-Col. Yerbury*). All B.M. 1892–192. INDIA: Calcutta, 1–17.xii.1908, 1 ♂, ex coll. Brunetti, B.M. 1927–184. KENYA: Teita Hills, Lumi River, xii.1912, 1 ♂. In the Coryndon Museum, Nairobi.

One male from Kanthalia has a paler abdomen than that of the holotype, especially the first segment, which is amber; the same specimen has the dark band on the posterior femora very much reduced. The male from Calcutta completely lacks the dark band on the posterior femora, which are pale amber. The male from Kenya has ten quite long scutellar teeth, each tipped with brown; the mesonotal pile is longer than in the holotype; the posterior femora are dark brown and the other legs are generally darker.

There are some rather puzzling differences in the genitalia, the typical form being illustrated in fig. 30 and an atypical form, which is commoner, shown in fig. 31. The typical form is only repeated in one of the males from Kanthalia. It seems that the typical form represents a more weakly sclerotised condition of the hypopygium; this weakness has apparently led to distortion involving extension of the parts during maceration in hot caustic potash.

The genitalia of the male from Kenya are almost identical with those of the males from Ceylon (fig. 31), but differ in that the apex of each style is broader, and the penis-sheath is not strongly angled below. The presence of this species in Africa is unexpected, and the unique specimen may represent a distinct subspecies which would be identified by the differences mentioned above. Unfortunately the specimen is in poor condition.

Shortest paratype 7·3 mm., longest paratype 9·0 mm.

Remarks.—All the specimens that I have of this species are strikingly large. It may be distinguished from the other species in the complex by the elongated antennae.

9. SUMMARY.

An extraordinary species of *Paragus*, *P. serratus*, was described from India by Fabricius in 1805; a closely related species, *P. crenulatus*, was described from China by Thomson in 1868; a third species, *P. azurea*, also closely related to *serratus*, was described from Sokotra by Hull in 1949. *P. serratus* has been thought to be distributed over most of the Oriental and Ethiopian Regions; a great variation in coloration has often been commented on. I have resolved *serratus* into *serratus s.str.* and four new species, *yerburiensis*, *auritus*, *pusillus* and *capricorni*. These are described, together with the allotype of *azurea*, and with *scrupeus*, a new subspecies of *azurea*. *P. serratus* (Fabricius) and *crenulatus* Thomson are redescribed. The male genitalia of each species are described and figured. *P. yerburiensis* and *serratus s.str.* are apparently confined to India; *auritus* is found in Ceylon, India and Africa; *capricorni*,

pusillus and *scrupeus* are African; *azurea* is apparently confined to Sokotra; *crenulatus* is widely distributed through the Oriental Region and Austro-Malayan Subregion. A note is included on the position of the complex within the genus. Keys are given, based on external and genitalic characters. A list is given of those characters which have proved to be of greatest taxonomic use.

10. ACKNOWLEDGMENTS.

I wish to thank Professor J. Omer-Cooper and Dr. E. McC. Callan for their invaluable criticism, advice and constant encouragement. I am most indebted to African Explosives and Chemical Industries Limited, and to the South African Council for Scientific and Industrial Research, for the award of grants enabling me to undertake this study. I wish also to express my appreciation to the following Institutions for placing their material at my disposal, and for the generous assistance which I have received: The British Museum (Natural History); The National Museum of Southern Rhodesia, Bulawayo; The South African Museum, Cape Town; Museé du Congo Belge, Tervuren; The Coryndon Museum, Nairobi; The Department of Entomology, Pretoria.

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THE FEEDING HABITS AND FOOD PREFERENCES OF ACRIDIDAE AND THE FACTORS WHICH DETERMINE THEM.

By L. H. Williams, Ph.D.

(Communicated by Professor O. W. Richards.)

Manuscript received 1st December, 1953.

(Read 5th May, 1954.)

With 25 Text-figures.

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1. Introduction.

The object of this work was to answer three questions: what plants are normally eaten by grasshoppers and locusts; how are they eaten, and why are they eaten in preference to others. Almost all past work on the feeding habits of Acrididae has been concerned with the rate of development on different foods and includes very little on the behaviour aspects of food selection. A brief review of the literature is included in the Discussion. This work was carried out at the Imperial College Field Station, Ascot, under the supervision of Prof. O. W. Richards.

2. Experimental Material and Methods of Rearing.

Several species of Acrididae occur in Berkshire and others were obtained from well-known localities. Much of the preliminary work was carried out on the two locusts, *Locusta migratoria* L. and *Schistocerca gregaria* (Forskål), while, later, stocks of grasshoppers were maintained under laboratory conditions throughout the year. The species, *Chorthippus bicolor* (Charpentier) (= *C. brunneus*), *C. albomarginatus* (De Geer) and *Gomphocerippus rufus* (L.) were most successful under artificial breeding conditions and were extensively used in experiments during the winter months. Other species studied were *Chorthippus parallelus* (Zetterstedt), *C. vagans* (Fieber), *Omocestus viridulus* (L.), *O. ventralis* (Zetterstedt), *Myrmeleotettix maculatus* (Thunberg), *Mecostethus grossus* (L.) and *Oedipoda caerulescens* (L.).

Young locust hoppers were kept in cages 13 inches long, 14 inches wide and 16 inches deep. The lid, sides and back were of wood, whilst the front was of glass; the floor was a sheet of metal which could be removed when cleaning out the cage. A door in the lid was used to introduce food. A 40 watt electric light bulb was suspended from the middle of the lid and branched twigs were arranged in the cage to allow the insects to reach the bulb. The floor was covered with a layer of coarse sand to a depth of about half an inch. Fourth and fifth instar hoppers were kept in larger cages, 24 inches cube. A 100 watt bulb was used in these cages. All locust stocks were kept in a Constant Temperature Room running at 29° C. and 68–70 per cent. relative humidity.

Young grasshoppers were kept in cylindrical celluloid cages with a metal base and perforated detachable lid. These cages were 8 inches in diameter and 15 inches deep. A 25 watt bulb was suspended from the lid. Large nymphs and adults were kept in small locust cages. All the grasshoppers were kept in the laboratory.

It was found that by switching off the lights in the cage for 12 hours on alternate nights, the length of life of the insects was increased, although the rate of development remained unchanged. Fresh grass was provided twice daily to the locusts and once daily to the grasshoppers. A soft grass, usually *Holcus mollis* L., was used. Water was provided only when the insects were being starved for experimental purposes.

Eggs were obtained freely from those species which normally lay their pods loosely in the soil. Females of these species oviposited in the layer of sand on the floor of the cages. Only a few pods were obtained from those grasshoppers which oviposit in grass tussocks. The egg-pods were stored in layers in containers of damp sand. The low temperature technique of Richards and Waloff was employed for breaking the diapause when stocks were required during the winter months.

3. Range of Plants Eaten.

During the late summer of 1951, about 200 hours were spent in watching grasshoppers in the field. Most of these observations were made on chalk pastures. Prolonged feeding on broad-leaved plants was never observed although a wide variety of such plants were nibbled. A total of 21 records was made of rejection by grasshoppers after chewing at the edge of a leaf. Among these was the moss, *Hypnum cupressiforme*. These observations were confirmed by field experiments in which adults of *Omocestus viridulus* were confined over a selection of growing plants. Each sample of natural vegetation was chosen so that it included several herbs as well as a choice of grasses. Twenty-three trials were made, but there was no evidence of prolonged feeding on any plants other than grasses, sedges and rushes and their allies, although signs of nibbling at the edges of the leaves of some plants indicated attempts at feeding (see Table I).

TABLE I.—*Field experiment in which 3 pairs of adult* Omocestus viridulus *were confined under each of 23 cages over natural vegetation to observe which plants were eaten.*

Type of plant.	Number of species.	Eaten (including nibbled).	Not eaten.
Grasses	11	29	0
Sedges	2	3	0
Luzula campestris	1	5	0
Rushes	1	1	0
Herbs	28	13 (nibbled only)	36
Mosses	2	0	5

Laboratory experiments also showed that, apart from sedges, rushes and their allies, plants other than grasses are seldom eaten by grasshoppers under normal conditions. However, hoppers of *Schistocerca gregaria* fed as readily on some herbs as on grasses. A few bitter plants, e.g. Ivy, *Hedera helix* L., were rejected, but others, the leaves of which are unpleasant to the human palate, e.g. Tomato, *Lycopersicon esculentum* Hill., were partly eaten.

When hoppers of *Locusta migratoria* were given 48 species of grass, they freely ate all but six. The species which were only partly chewed were : *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.), *Brachypodium sylvaticum* (Huds.), *Briza minor* L. and *Bromus erectus* Huds. Later, these grasses were offered to adults of *Chorthippus albomarginatus*, but only the *Arrhenatherum* was rejected. Even this was eaten in field trials in preference to broad-leaved plants when no other grasses were available.

Nevertheless a definite preference was shown for certain species of grass, as was shown by presenting hungry *Locusta* hoppers with a choice of two grasses and counting the number feeding on each at five minute intervals for a total of forty minutes. Each grass was chopped up coarsely and placed in a heap on a piece of paper to ensure that approximately the same quantity was introduced. The eight grasses used in this trial were : *Arrhenatherum elatius* (L.), *Anthoxanthum odoratum* L., *Deschampsia flexuosa* (L.), *Agropyron caninum* Beauv., *Alopecurus pratensis* L., *Bromus sterilis* L., *Holcus mollis* L. and *Festuca ovina* L. Each species of grass was tested four times with each of the other seven, the tests being repeated on different batches of insects. The relative positions of the alternative choices were exchanged in successive trials. The order of the grasses as listed above approximates to the order of acceptability as food to the hoppers, *Holcus* and *Festuca* being the most preferred. Thus, when the choice is between *Deschampsia flexuosa* and *Arrhenatherum elatius*, the *Deschampsia* is selected, but when it lies between *Deschampsia* and *Agropyron caninum*, the *Agropyron* is usually chosen.

Similar experiments were carried out on the adults of five species of grasshopper, the grasses used, in order of preference being : *Arrhenatherum elatius*, *Anthoxanthum odoratum*, *Nardus stricta* L., *Molinia caerulea* (L.), *Holcus mollis* *Brachypodium sylvaticum*, *Festuca ovina* and *Dactylis glomerata* L. (most preferred).

Although the grass blade is normally eaten, in captivity grasshoppers will feed quite readily on the young inflorescences. When the flower spike is fully opened or setting seed, the glumes are usually too tough to be easily eaten. Feeding on the flower was only seen on two occasions in the field (both on *Festuca*

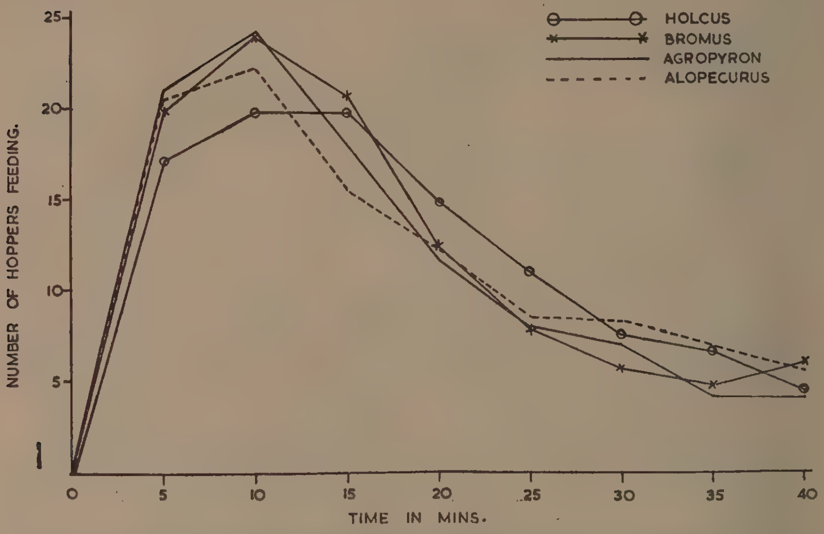


FIG. 1.—Experiment to show the time spent by *Locusta* hoppers when feeding on broad-leaved grasses. Grasses used: *Holcus mollis*, *Bromus sterilis*, *Agropyron caninum* and *Alopecurus pratensis.*

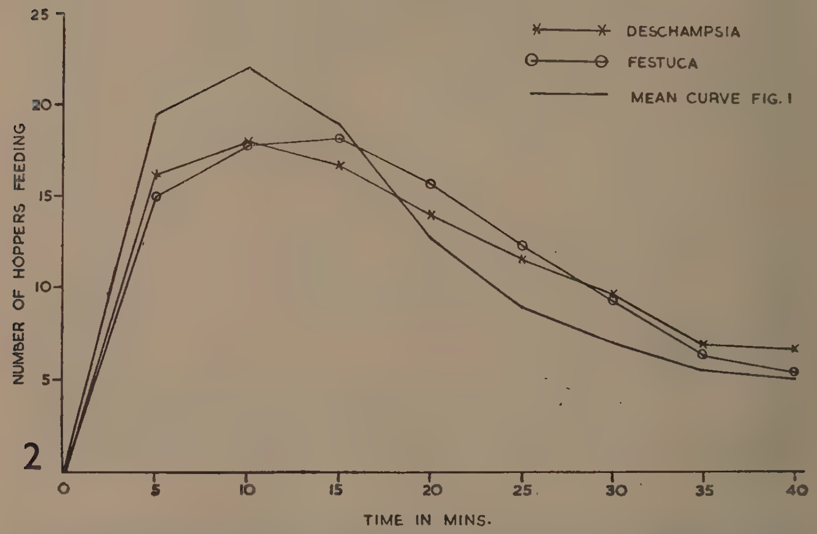


FIG. 2.—Experiment to show the time spent by *Locusta* hoppers when feeding on narrow-leaved grasses. Grasses used: *Deschampsia flexuosa* and *Festuca ovina.* For comparison, the mean of the four curves in fig. 1 is also shown.

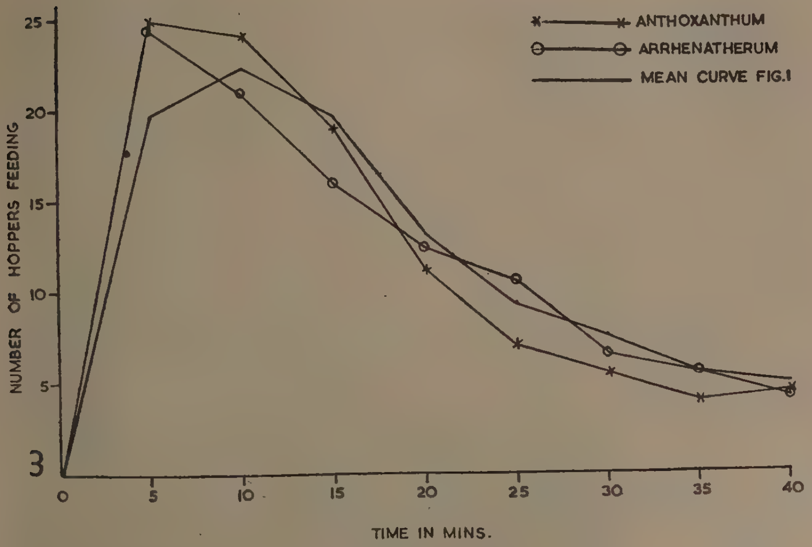


FIG. 3.—Experiment to show the time spent by *Locusta* hoppers when feeding on unpalatable grasses. Grasses used: *Anthoxanthum odoratum* and *Arrhenatherum elatius*. For comparison, the mean of the four curves in fig. 1 is also shown.

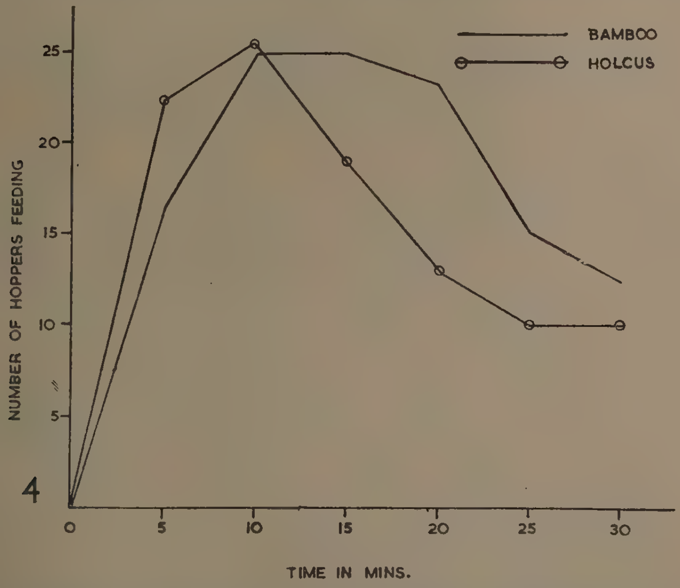


FIG. 4.—Comparison between the time spent by *Locusta* hoppers feeding on *Holcus mollis* and on bamboo (*Bambusa* sp.). The curve for bamboo is very like those for the acicular grasses, *Festuca* and *Deschampsia* (see fig. 2).

ovina), but most observations were made on closely grazed turf. Fifth stage hoppers of *Locusta* fed quite readily on grated or thinly-sliced portions of the storage organs of swedes, carrots and parsnips but only nibbled at beetroot and potatoes.

Observations on the nymphs of grasshoppers suggest that they have the same food preferences as the adults. The coarser species of grass may be too tough for the jaws of very young nymphs and are less freely eaten.

4. FEEDING HABITS.

(i) *Method of Feeding.*

When food is introduced into a cage containing a hungry grasshopper, the insect first orientates itself to face the food, then walks towards it. As in all normal locomotion, the antennae are periodically lowered to touch the surface of the substrate. On reaching the food the grasshopper usually first "feels" it with its antennae, then the head is lowered until the surface of the labrum touches the leaf. Next, the tips of the palpi are lightly brought to bear on the leaf a number of times in rapid succession and finally the insect closes its mandibles on the edge of the blade, taking first a small bite which is thoroughly chewed in the buccal cavity and then either continues to feed in a systematic manner or moves away to sample another leaf. A second exploratory bite is sometimes made. Pieces of the leaf are eaten with a downward action which removes crescentic areas. During the actual biting movements the palpi are usually held a short distance above the leaf surface, but they may sometimes be occasionally lowered to touch the leaf. At the end of each "bite" the grasshopper raises its head, and, after "feeling" again for the edge of the blade with its palpi, begins to remove another crescent. Frequently the fore legs are used to steady the grass, being held just in front of the labrum, that is, in a position near the upper limit of the feeding area.

(ii) *Duration of Meals.*

It will be shown later that leaf shape has little effect on food selection by Acrididae. However, leaf form and toughness undoubtedly have a considerable influence on the time taken in feeding. Grasses which have tightly rolled or very narrow leaves, e.g. *Festuca ovina*, *Deschampsia flexuosa*, *Nardus stricta*, are more difficult to chew than the species with flat ribbon-shaped blades, although they are freely eaten, and this is of great importance when conducting food preference experiments which involve numerical estimations.

Fig. 1 shows the number of *Locusta* hoppers feeding on each of a series of four broad-leaved grasses at each five-minute period of an experiment, expressed as a percentage of the total count on each for the whole 45 minutes' duration of the experiment. It will be seen that the highest total of feeding hoppers was after 10 minutes. Fig. 2 shows the results obtained in a comparable experiment when the acicular grasses, *Festuca ovina* and *Deschampsia flexuosa* were used. In this case the pronounced peak of fig. 1 is not seen, which indicates that a longer time was spent in feeding. It is interesting to compare these graphs with those for the unpalatable grasses *Arrhenatherum elatius* and *Anthoxanthum odoratum* (fig. 3). These show an early peak, after only five minutes, after which the number of insects feeding dropped very sharply.

In these instances the variation in time taken over meals is due to differences in the shape of the leaves. Toughness has a similar effect on the duration of feeding, as shown in fig. 4, which compares the feeding times on *Holcus mollis* and *Bambusa*. The *Bambusa* is probably about six times as tough as the *Holcus*. (See p. 435).

Longer time being taken when feeding on grasses which are tough or more difficult to chew makes these grasses appear more favourable as food than they really are.

The duration of meals on the same food varies within quite wide limits. Observations made in the laboratory on three species of grasshopper suggested that males spend slightly longer in feeding, whereas females feed more frequently. The figures also indicated differences in the duration of meals by different species of grasshoppers. Thus, *Gomphocerippus rufus* appears to spend a longer time feeding than *Chorthippus albomarginatus*.

5. MORPHOLOGY OF MANDIBLES AND CROP.

A. *Mandibles.*

A study was made of the mandibles and other mouth parts of the eleven British species of Acrididae and of *Locusta migratoria* and *Schistocerca gregaria*.

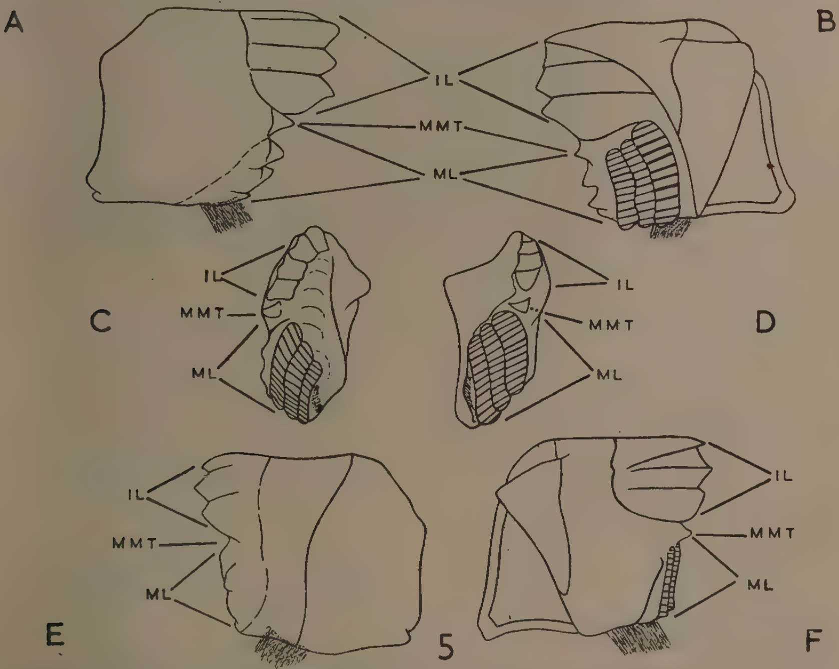


FIG. 5.—Diagrams to show the principal features of Acridid mandibles. A, B, C, left mandible: (A) Antero-lateral view; (B) Postero-lateral view; (C) Mesial view. D, E, F, right mandible: (D) Mesial view; (E) Antero-lateral view; (F) Postero-lateral view. *il*, incisor lobe. *mmt*, median molar tooth. *ml*, molar lobe.

Important morphological differences were observed only in the mandibles. Of these species, ten are almost exclusively grass feeders and *Schistocerca gregaria* is a mixed feeder. The feeding habits of *Chorthippus vagans* and *Oedipoda caerulescens* were not studied.

Isely (1944) distinguishes three main types of Acridid mandibles: broad-leaved plant feeding, grass feeding and mixed plant feeding. Intermediates occur between each type. Of the mandibles studied here, those of *Schistocerca* are of the mixed feeding type and those of *Oedipoda caerulescens* and *Chorthippus vagans* have features intermediate between those of the mixed feeders and the purely graminivorous species. The mandibles of the remaining species are typically graminivorous and have only minor specific differences (figs. 6–18). The considerable differences between the mandibles of the four British species of *Chorthippus* are interesting from the systematic point of view. Similar differences in the members of a genus were noted by Isely.

The asymmetry of grasshopper mandibles and the curious feature that the left mandible overlaps the right have been discussed and figured by Uvarov and by Snodgrass (1928). Each mandible consists of a main body and two lobe-like regions, the biting or incisor lobe and the grinding or molar lobe (fig. 5, A–F). The teeth and ridges of the right mandible fit into those of the left.

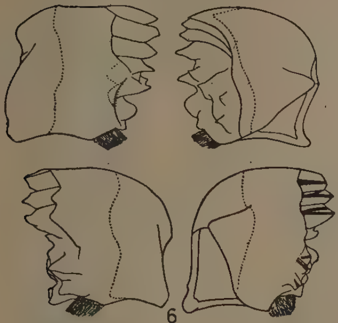
Wherever possible, several examples of each species were examined. In most cases, only slight differences were observed between specimens of the same species. These consisted of variation in the area of darkening (where the jaw is fully exposed and not covered by integument or the overlap of the opposite mandible) and in the degree of sharpness of the incisor teeth. In old individuals the teeth become broken and worn through constant use so that young adults were examined wherever available. *Chorthippus bicolor* and *C. parallelus* hoppers were also examined in every stage. The mandibles in these species do not undergo any modifications with nymphal development, although the teeth are sharper in many young individuals than in the adult stage, doubtless because they have been less used.

The characters of the two types of mandibles are summarised here.

	Herbivorous type.	Graminivorous type.
1.	The incisor teeth are pointed.	The incisor teeth are relatively blunt.
2.	The incisors of the left jaw are short.	The incisors of the left jaw are long.
3.	The jaws overlap and interlock considerably, and the distal edge of the right incisor lobe is not bevelled.	The left jaw only slightly overlaps the right and the distal edge of the right incisor lobe is bevelled.
4.	The molar lobes consist of several teeth surrounding a cavity.	The molar lobes consist of a series of ridges and furrows.
5.	Marginal molar teeth are well developed.	Marginal molar teeth are poorly developed.

B. *The Crop.*

The grasshopper crop is a muscular organ of considerable dimensions and is the centre of the digestive processes, besides functioning as a storage chamber. Internally the wall of this organ is thrown into a series of longitudinal ridges.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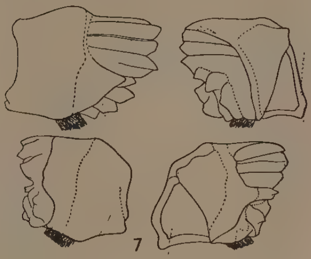
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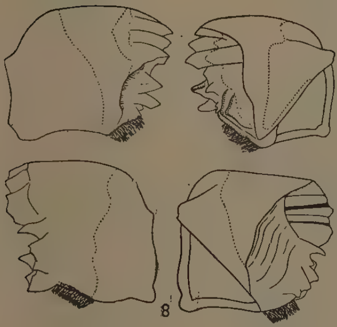
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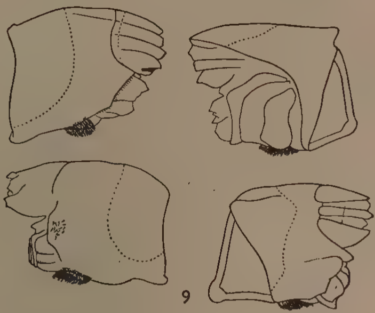
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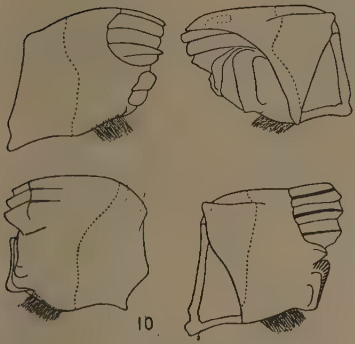
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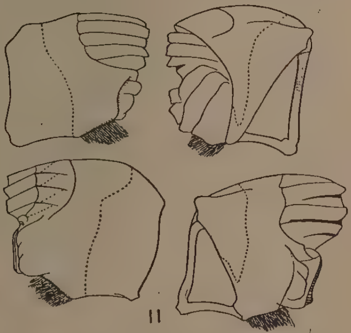
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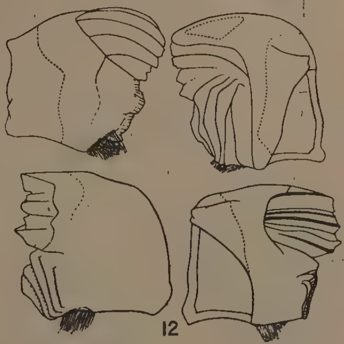
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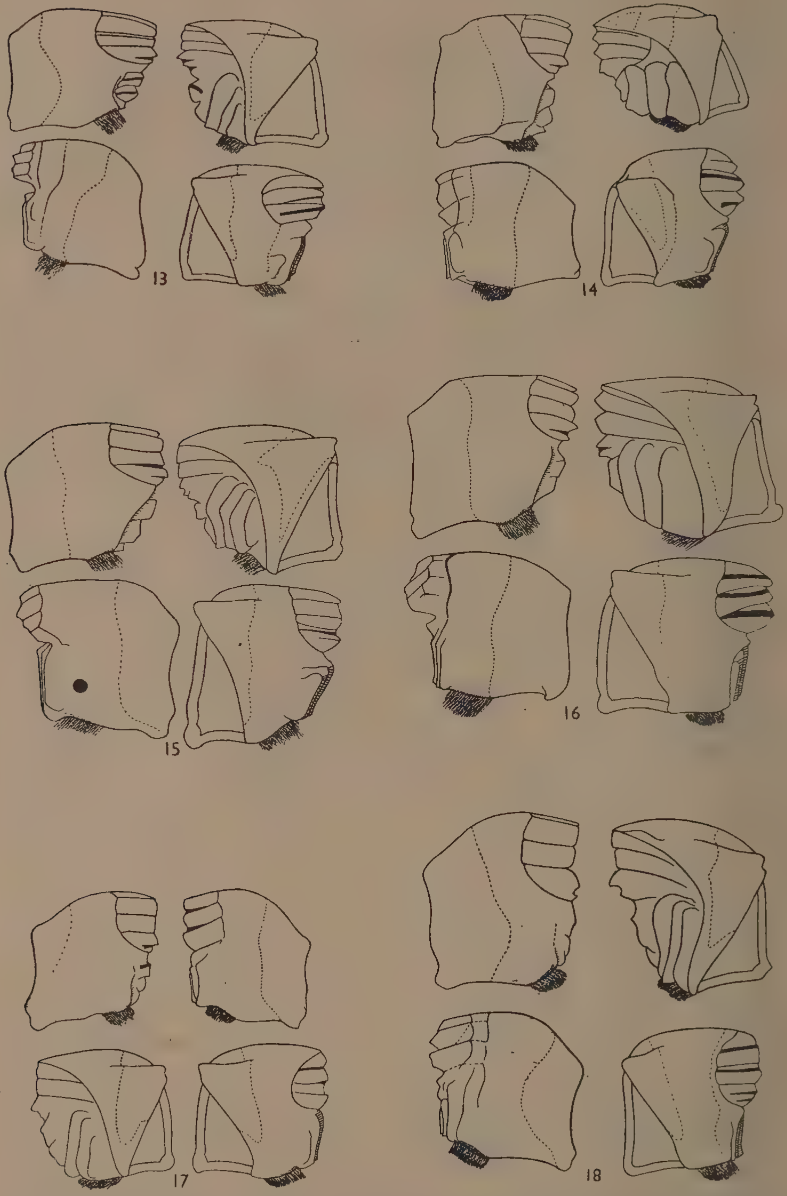
FIGS. 6–12.—Antero-lateral and postero-lateral views of the left and right mandibles of: (6) *Schistocerca gregaria* Forskål. (7) *Chorthippus vagans* Fieber. (8) *Oedipoda caerulescens* L. (9) *Mecostethus grossus* L. (10) *Chorthippus parallelus* Zetterstedt. (11) *Stenobothrus lineatus* Panzer. (12) *Locusta migratoria* L.



FIGS. 13–18.—Antero-lateral and postero-lateral views of the left and right mandibles of: (13) *Myrmeleotettix maculatus* Thunberg. (14) *Chorthippus bicolor* Charpentier. (15) *Omocestus viridulus* L. (16) *Omocestus ventralis* Zetterstedt. (17) *Chorthippus albomarginatus* De Geer. (18) *Gomphocerippus rufus* L.

Each ridge is armed with numerous minute conical spines throughout the anterior two-thirds of its length. Anteriorly there is a pair of lateral areas where the spines are specially well-developed on rather broad elevations of the wall. There may be several rows of spines on each of these ridges (fig. 19).

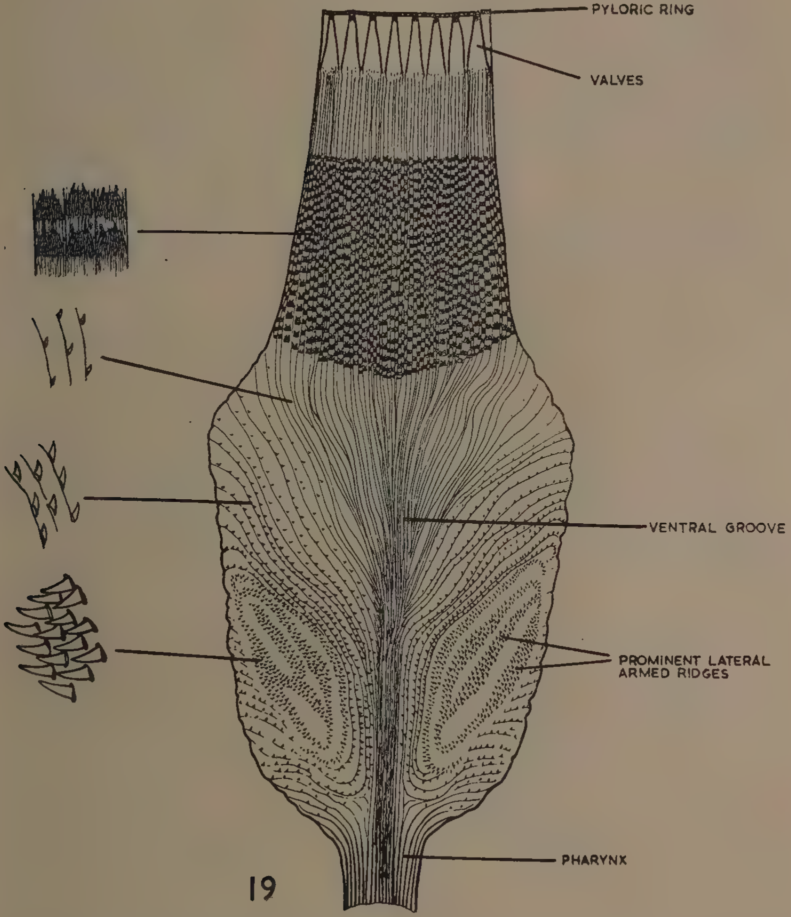


FIG. 19.—Internal armature of the crop of *Locusta migratoria* as exposed by slitting the dorsal wall longitudinally and pinning back the cut edges.

Examination of the prominent lateral ridges of the crop of each of the eleven British species of Acrididae showed that there are well-marked differences between some of them. On the whole, the armature was better developed in the female sex than in the male. There was considerable variation between individuals of the same species and, sometimes, even between opposite sides of the crop of the one individual. The two species where the teeth are most poorly developed, *Oedipoda caerulescens* and *Chorthippus vagans*, are those with the most prominent mandibular teeth. It is necessary to study more types before a correlation can be suggested.

6. FACTORS WHICH INFLUENCE THE FINDING AND SELECTION OF FOOD.

A. *Habitat.*

The differences in the general composition of the vegetation between the different kinds of habitat occupied by British grasshoppers might suggest that the limitation of the species to these habitats is directly connected with the distribution of essential food plants. From a consideration of the different habitats occupied by *Myrmeleotettix maculatus*, including dry heaths, chalk downs, dune slacks, etc., it follows that this grasshopper must feed regularly on several different kinds of grass. In this investigation grasshoppers were never found in any situation where grass was not present, and most grasses have been shown to be suitable as food-plants to these insects.

From this it seems probable that it is the structure of the vegetation, rather than its composition, which limits the distribution of our grasshopper species.

B. *Physical Properties of the Food.*

(i) *Toughness.*—Fig. 20 is a diagram of the apparatus which was constructed to measure the comparative toughness of different grasses. It consists of a small box of stout paper with a No. 10 entomological pin pushed through its base. A length of fine glass tubing slightly shorter than the pin was pushed into the cork bung of a 3 × 1 in. specimen tube. The blade of grass to be

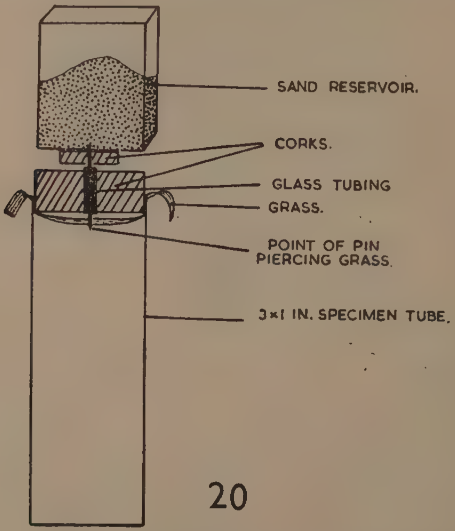


FIG. 20.—Diagram of apparatus used to measure the relative toughness of different kinds of grass.

measured was stretched across the mouth of the tube, then the cork was inserted carefully so that the grass remained taut. Next, the pin was introduced into the glass tubing. Silver sand was then slowly poured into the box until the point of the pin just penetrated the blade of grass. The sand was then removed and weighed. The apparatus was made more rigid by glueing a small flat piece of cork to the underside of the paper box. Some of the results obtained with this apparatus are shown in Table II.

TABLE II.—*The relative toughness of some British grasses measured by the "sand reservoir" method. The figures represent the weight of sand in grams required to push the point of the pin through the blade.*

	Holcus mollis.	*Bromus sterilis.*	*Anthoxanthum odoratum.*	*Alopecurus pratensis.*	*Arrehnatherum elatius.*	*Agropyron caninum.*	*Deschampsia flexuosa.*
Number of Measurements .	10	10	10	10	10	10	10
Mean . . .	4·21	4·47	5·50	5·94	6·03	6·36	12·22
Standard deviation	0·104	0·109	0·067	0·210	0·117	0·093	4·242

The form of *Deschampsia flexuosa* leaves which are thick and leathery although very narrow, proved difficult to measure accurately as the pin sometimes penetrated the tissues obliquely, causing some discrepancy in the results. The tests were all carried out at approximately the middle of the leaves, the leaves chosen being of more or less the same age and condition for each species.

When first instar *Locusta* hoppers were fed with bamboo it was noticed that feeding was confined to near the tips of the leaves, although exploratory nibbles were made on the edge along the whole length of the leaf. It seemed that the insects were unable to insert their small jaws in the thicker parts of the blade. This behaviour was confined to the young hoppers, in later instars they fed quite readily in all positions on the leaves.

Locusta hoppers were taken straight from the egg and were daily given a choice of bamboo and *Holcus* leaves until most of them reached the fifth instar. The number of hoppers feeding on each food was counted at five-minute intervals for half an hour. The sums of the six readings obtained each day are set out in Table III.

These figures show that the early instars have a definite preference for *Holcus*, although older hoppers showed no preference for either grass. The apparent slight preference for *Bambusa* by the fourth and fifth instars is probably due to the extreme toughness of the grass and hence the longer time grasshoppers spend feeding on this species. By the "sand reservoir" method the toughness of *Bambusa* was 25+ units and *Holcus mollis* was 4+ units.

In the case of British grasshoppers toughness is probably of importance in food selection only for young hoppers. No British grass which British Acrididae are likely to encounter is as tough as bamboo, but newly hatched grasshopper nymphs are very much smaller than those of *Locusta*.

Examination of particles in the frass gives additional evidence of the effect of toughness of food. Preliminary work showed that the gut of *Gomphocerippus rufus* adults is completely emptied within 24 hours of taking a meal. Adult males of this species were deprived of food for 48 hours and then fed in turn on a number of different kinds of grass of different toughness. The frass pellets which were subsequently voided were examined microscopically and the size of the particles in each was measured with a micrometer eye-piece. Histograms of particle size are included (fig. 21A, B, C) for the grasses, *Bambusa*, *Dactylis glomerata* and *Holcus mollis*. There are considerably more particles in the smaller size groups in the faecal pellets from *Bambusa* than in those from *Dactylis* and *Holcus*. This suggests that as this grass is exceptionally tough, grasshoppers find it difficult to chew and consequently bite off only small fragments.

Table III.—*The relative preference of* Bambusa *and* Holcus *to* Locusta *hoppers of different ages.*

		Percentage of Feeding hoppers which were feeding on *Bambusa*.		Average percentage on *Bambusa*/instar.	
Day.	Instar.	Expt. 1.	Expt. 2.	Expt. 1.	Expt. 2.
1	1	24·2	.	18·4	.
2	1	21·1	27·8		
3	1	9·8	20·2		
4	1 and 2	32·4	9·4	25·2	18·9
5	2	18·9	19·8		
6	2	24·4	27·5		
7	2 and 3	45·5	49·2	44·9	33·4
8	2 and 3	56·0	19·3		
9	3	33·3	31·8		
10	3 and 4	49·4	43·8	58·4	50·9
11	3 and 4	62·5	50·5		
12	3 and 4	47·7	50·5		
13	4	66·6	70·8		
14	4	65·9	39·0		
15	4 and 5	46·3	50·9	.	.
16	4 and 5	.	56·8	.	.

(ii) *Texture of leaf surface.*—Hungry grasshoppers do not hesitate to nibble the leaves of a very wide variety of different plants, some of which are densely hairy while others are perfectly glabrous. Table IV gives the results of an experiment in which notes were made on the time taken to elicit a biting response in starved adults of *Gomphocerippus rufus* when offered a number of different plants. Each insect was watched for 15 minutes and " no response " was recorded if no attempt to feed was made within this period. A " biting response " was judged as the opening and closure of the mandibles on the edge of a leaf. With two exceptions, responses were observed with equal frequency on plants with very different surface textures and there was no apparent discrimination between grasses and other plants. The exceptions were strips of white paper and shoots of the Gymnosperm, *Cupressus lawsoniana*. *Cupressus* contains strongly aromatic resins which may be repellants to Acrididae. In other experiments (see p. 440) paper was partly eaten.

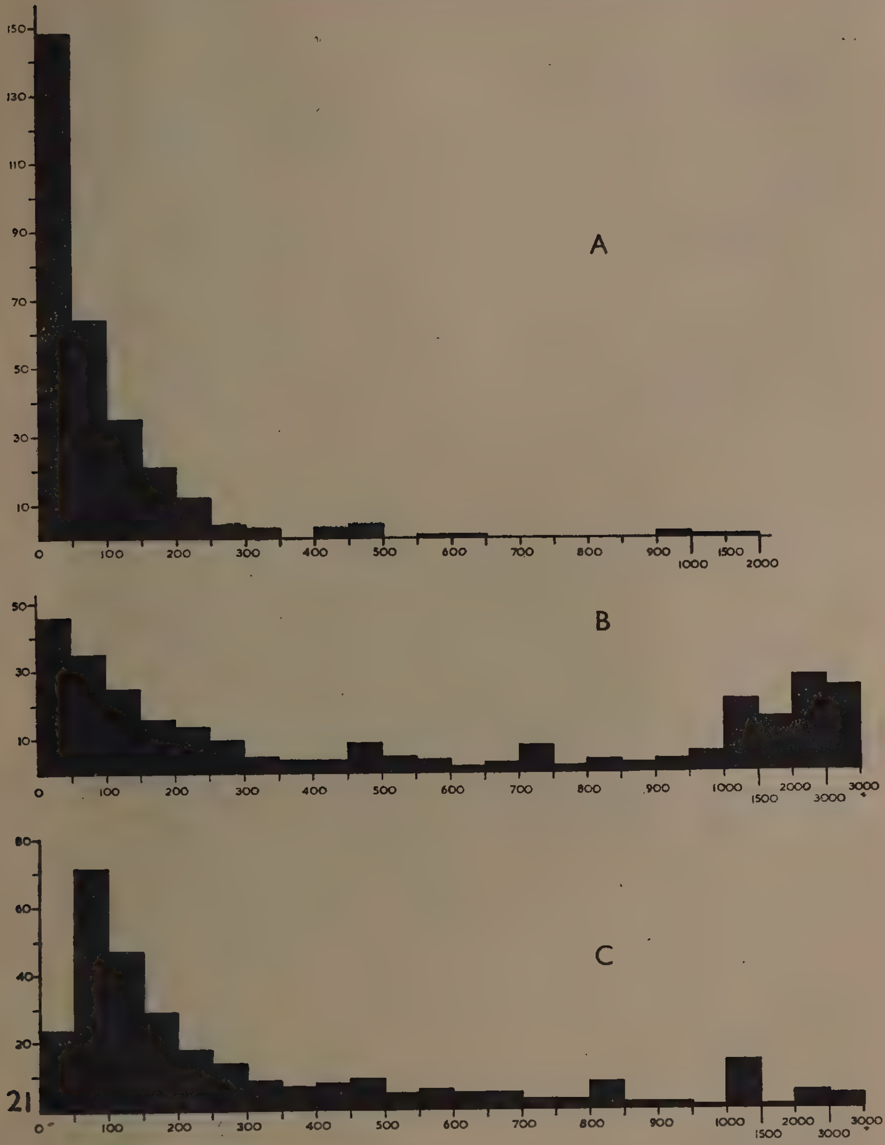


Fig. 21.—Histograms showing the number of particles of different size groups in the frass of adults of the grasshopper *Gomphocerippus rufus* after they had been fed on three grasses. Particles measured with a graduated eye-piece. 300 measurements made on each kind of pellet. 3,500 units of particle size = 1 sq. mm. Toughness of grasses measured by the "sand reservoir" method and expressed in gm. weight required to push pin through leaf-blade.

(A) Bamboo (*Bambusa* sp.)—Toughness 25 + units.
(B) *Dactylis glomerata*—Toughness 7·5 units.
(C) *Holcus mollis*—Toughness 4·2 units.

TABLE IV.—*Experiment to show the time taken to elicit a biting response in adults of* Gomphocerippus rufus *when offered plants, etc. with different surface textures.*

Experimental material.	Number of trials.	Number of responses (in 15 mins.).	Average time before response (mins.).
Grasses.			
Holcus mollis	20	17	2·4
Bambusa sp.	10	9	5.0
Arrhenatherum elatius	10	9	3·7
Deschampsia flexuosa	10	8	3·9
Other plants.			
Juncus effusus	10	8	2·3
Digitalis purpurea	10	8	1·8
Rhododendron ponticum	10	10	4·3
Anchusa sempervirens	10	8	1·4
Agrostemma coronaria	10	8	2·5
Chrysanthemum parthenium	10	8	3·6
Cupressus lawsoniana	10	0	.
Other materials.			
Raffia (yellow)	10	6	1·7
White smooth paper	10	0	.

(iii) *Leaf shape.*—As biting responses can be induced on broad, narrow, entire and dissected leaves, the shape of the leaf appears to be of no importance in food selection.

(iv) *Moisture content.*—Criddle (1935) drew attention to the fact that certain plants are much more readily consumed during hot weather than at other times of the year. He suggested that some plants are selected at times by insects because of their high moisture content. This appears to be supported by the present observations, for it was found that when grasshoppers were deprived of water as well as food for 48 hours, they could be induced to feed on a number of succulent plants which previously they would only slightly nibble.

TABLE V.—*Experiment to compare the area of* Sonchus *leaves eaten by adults of* Chorthippus parallelus *when the leaves are fresh and when they have been dried for different periods. Measurement of area in square inches.*

	Fresh leaves.		Dried leaves.			
Day.	Number of signs of feeding.	Area eaten.	Number of signs of feeding.	Area eaten.	Total area consumed.	Relation between area eaten fresh/dry.
1	39	2·41	58	1·16	3·57	2·08
2	42	2·23	33	0·73	2·96	3·05
3	47	2·86	19	0·12	2·98	23·83

Leaves of *Sonchus arvensis* were collected and lightly pressed between sheets of botanical drying paper to keep them flat. Adults of *Chorthippus parallelus* were given a choice of fresh and dry *Sonchus* leaves on three consecutive days. On the first day, the pressed leaves were still soft to the touch whilst by the third day of drying, they had become rather brittle. The leaves were placed in an upright position in the cage and were left for three hours after which they were removed and the area of leaf surface consumed was measured with squared paper. Twenty-four grasshoppers were used, all of which had been deprived of food and water for 12 hours, during part of which time they had been exposed to bright sunshine.

The results are summarised in Table V.

As the number of signs of feeding on dry *Sonchus* decreased as the leaves became drier, it indicates that the insects showed less perseverance in trying to locate suitable feeding positions.

To demonstrate the importance of moisture content in the case of grasses an experiment was carried out as follows: Long blades of *Holcus lanatus* were pressed for one, two and three days, then stretched between a stiff cardboard frame, each end being held in position by means of a small piece of adhesive paper. Each day a second frame was prepared by using fresh blades of *Holcus*. The two frames were placed on opposite sides of a cage containing twenty-four adult *Chorthippus parallelus* which had been deprived of food and water for at least 12 hours, during part of which time they had been in bright sunlight. Tests showed that these insects immediately swallowed droplets of water when these were offered on a needle. The cage was rotated every 30 minutes to offset any bias due to uneven illumination. After three hours the frames were removed and the areas of leaf surface which had been consumed were measured with squared paper. Records were also made of the number of signs of attempted feeding in which the areas eaten were too small to be measured, i.e. they were less than 0·01 sq. in. This was followed by a second test in which dry *Holcus* leaves which had been soaked in rain water for two hours were substituted for the dry *Holcus*. A second batch of 24 adult grasshoppers from the same stock cage as in the previous trial was used. The results are given in Table VI.

TABLE VI.—*Experiment to compare the feeding of* Chorthippus parallelus *adults on fresh, dry and dry re-wetted blades of* Holcus lanatus. *Measurements of areas eaten are in square inches. "Per cent. small of total" refers to the percentage of small feeds (i.e. those less than* 0·01 *sq. in.) in the total number of indications that feeding had taken place.*

		Fresh *Holcus*.			Dry *Holcus*.		
Day.	Number of feeds.	Area eaten.	Per cent. small of total.	Number of feeds.	Area eaten.	Per cent. small of total.	Relation between area eaten (fresh/dry).
1	38	2·33	26	77	1·60	62	1·46
2	25	2·08	28	43	0·95	63	2·19
3	56	3·18	18·5	97	0·98	60	3·19
		Fresh *Holcus*.			Dry *Holcus* re-wetted.		
1	20	1·24	10	51	1·65	41·2	0·75
2	25	1·09	12·5	40	1·36	48	0·80
3	25	2·28	20	43	1·29	48·8	1·77

The difference between the readiness with which dry re-wetted grass and dry grass are eaten strongly suggests that the former is preferred for its high superficial water content. On the first and second days more of this grass than the fresh *Holcus* was eaten. On the other hand, more exploratory nibbles were made on the re-wetted grass than on the fresh *Holcus*, but rather fewer than on dry *Holcus*. A comparison between the fresh and dry grass shows that as the grass dries out less of it is eaten. By stretching the blades on a frame, they are prevented from becoming limp, as in that condition they are not easily eaten by grasshoppers.

Further evidence of the importance of moisture content was provided by experiments in which paper was used as the experimental material. Nymphs of *Chorthippus parallelus* were, in turn, offered green paper, white paper and the same after being moistened. Records were made of the time before the first biting response was initiated and of the number and duration of the feeding periods during a spell of five minutes. The results are summarised in Table VII.

Table VII.—*Experiment to compare the biting response behaviour of nymphs of* Chorthippus parallelus *when offered different types of paper.*

	After 4 hours' starvation.				After 8 hours' starvation.		
	White dry.	Green dry.	White damp.	Green damp.	Green dry.	Green damp.	White damp.
Number of trials	10	10	10	10	10	10	10
Number of trials in which a response was noted	0	0	4	5	7	9	8
Average time before first response (secs.)			135	132	77	40	22·5
Total number of responses in 5 min.			7	9	17	32	22
Average number of responses in 5 min.			1·75	1·8	2·43	3·56	2·75
Total duration of responses (secs.)			42	106	107	367	314
Range of duration of responses (secs.)			2–12	2–77	2–24	2–84	2–54
Average duration of responses (secs.)			6	11·8	6·3	11·5	14·3

(v) *Colour.*—Although different kinds of grass vary in colour from pale to very dark green, there is no evidence that this is a factor of any importance in deciding food selection. There was no significant difference between the number of nymphs of *Chorthippus parallelus* which attempted to feed on a heap of pale yellow-green paper and those on dark green paper and grasshoppers quite readily attempted to nibble at pieces of plain white paper (see Table VII).

Leaves of *Phalaris arundinacea* var. *variegata* were collected and the yellow regions separated from the normal green. These were offered as a choice to nymphs of *Chorthippus parallelus*, six counts of the number of insects feeding on each piece being made at five-minute intervals. There is no significant difference between the two types.

	Green part.	Yellow part.	Total.
Trial 1	48	34	82
2	45	49	94
3	36	42	78
4	43	41	84
Total	172	166	338
Average	43	41·5	

C. *Senses and Sense Organs.*

In the following experiments bamboo was used as the standard food as the shape of its leaves permits easy measurement with squared paper. The narrow blades of most grasses cannot be measured accurately in this way. Bamboo remains fresh longer than most of the common British grasses when in the Constant Temperature Room.

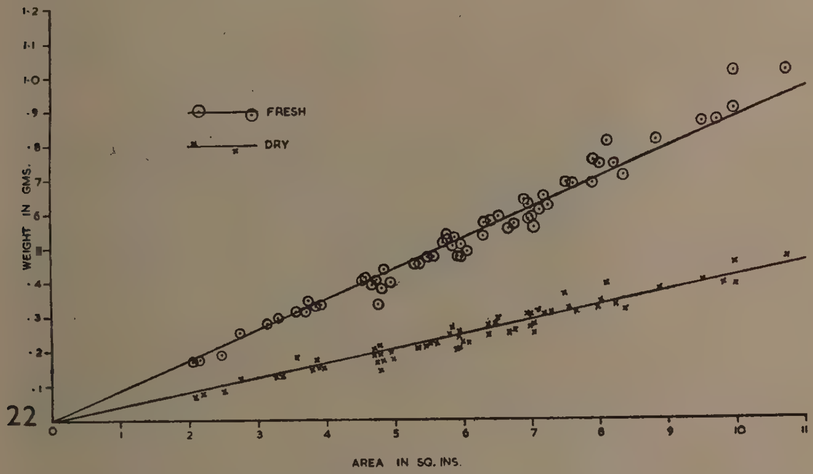


FIG. 22.—The relationship between surface area and weight (fresh and dry) of bamboo leaves. The lines represent the means of 60 measurements. Area, range 0–11 sq. in. Weight, range 0–1·2 gm.

The relationship between surface area and fresh and dry weight of bamboo leaves is expressed graphically in Fig. 22. The average weight per square inch of the sixty leaves used in this determination was: fresh 0·089 gm., dry 0·042 gm. As the points all lie near to the mean line it was considered to be justified to use surface area as a measurement of the quantity of food eaten. The leaves used in the experiments were all of approximately the same size (*c.* 6 square inches).

(i) *The eyes and sight.*—A series of experiments was carried out on adult locusts to determine the importance of the different sense organs in the location of food. The results are summarised in Table VIII and the experimental technique and results will be described in the appropriate sections. The following is a description of the technique used to assess the part played by the eyes.

Table VIII.—*Experiments with adult locusts to test the effect on food consumption of amputating the antennae, amputating the palpi, and blackening over the eyes. One experiment was also carried out on locusts in which all these sense organs had been treated. The figures in Experiment* 1 *are sq. in. of grass eaten, those in Experiments* 2 (*A and B*) *weight of dry frass in gm.*

No. of days from start of Expt.	Experiment 1 (4 locusts).				All sense organs removed or blacked out.	Experiment 2.							
						A. (8 locusts).				B. (10 locusts).			
	Control cage.	Eyes blacked out.	Antennae removed.	Palpi removed.		Control cage.	Eyes blacked out.	Antennae removed.	Palpi removed.	Control cage.	Eyes blacked out.	Antennae removed.	Palpi removed.
1	×	×	×	×	×	×	×	×	×	×	×	×	×
2	×	×	×	×	×	×	×	×	×	×	×	×	×
3	10·46	6·88	13·09	8·43	0·81	0·96	0·30	0·33	0·74	×	×	×	×
4	0·03	2·64	9·29	11·05	0·87	1·48	0·51	0·56	1·17	3·85	3·55	3·84	2·34
5	15·73	1·91	27·04	13·29	3·65	0·98	0·51	0·595	0·77	6·08	5·33	4·46	4·24
6	18·8	5·82	16·98	13·48	5·30	1·165	0·51	0·52	0·96	4·43	3·58	3·31	3·64
7	16·62	4·57	8·96	17·28	4·53	0·965	0·52	0·48	0·97	4·65	2·98	3·44	3·64
8	18·44	3·21	7·12	16·23	6·90	1·265	0·74	0·84	1·25	4·77	3·91	0·60	3·37
9	×	×	×	×	×	1·01	0·84	0·925	1·43	×	×	×	×
10	×	×	×	×	×	1·125	0·80	1·295	1·32	×	×	×	×
A. Area eaten Total B.C. Weight of Frass.	79·46	25·03	82·48	79·77	22·06	8·94	4·73	5·54	8·61	23·79	19·35	15·65	17·22
Mean/Day/Locust	3·31	1·04	3·435	3·32	3·677	0·140	0·074	0·087	0·135	0·476	0·387	0·313	0·344

" × " signifies no experiment carried out on this day to allow insects some time to recover from shock of treatment.

The eyes of two pairs of adult *Locusta migratoria* were blackened over with cellulose paint applied thickly with an artist's brush. The insects were put in a large cage with a few shoots of bamboo in one corner. To reach the bamboo, the locusts had either to climb up the side of the cage or jump on to it from the floor. The surface area of leaf eaten every 24 hours was taken as the measurement of feeding. The first measurement was made on the third day after the paint was applied. A similar cage containing two pairs of normal locusts was used as a control (Experiment 1). All the insects used were of the same age. In a second experiment four pairs of locusts were used and the dry weight of frass produced every 24 hours was used to assess the amount of feeding (Experiment 2A). A third experiment (2B) was also carried out using five pairs of locusts and measuring the dry weight of frass.

These results indicate that less feeding was done by the locusts when their eyes were covered. This could be interpreted as difficulty in finding the food or reduction in activity due to the effect of "darkness," when less food would be required to maintain normal health. To test this an experiment was carried out using two batches of normal locusts, one batch being kept permanently illuminated while the other was in total darkness. Four adults were used in each cage and an abundant supply of bamboo shoots was maintained. The results are shown in Table IX.

These results show that the effect of blackening over the eyes is probably to reduce activity and, consequently, the consumption of food is less.

One side of a square glass cage was covered with a vertical pattern of black stripes on a white background. The opposite side of the cage was covered in turn with a sheet of white paper, black paper and a sheet with horizontal black stripes. Adults of *Gomphocerippus rufus* were introduced into the cage singly and watched to see whether they were attracted to one side of the container. Each trial was carried out 60 times and the cage was turned round after every five trials so as to eliminate any bias due to uneven illumination. The results set out in Table X show a well-marked preference for the side with vertical stripes. In later experiments of this kind, adults of *Chorthippus parallelus* were used. It was found that the insects showed no preference for vertical stripes over stripes at an angle of 45 degrees, but that a slight preference was shown over stripes which sloped at only 20 degrees from the horizontal.

TABLE IX.—*Experiment to test the effect of darkness on the food consumption of adult locusts.*

Day.	Area eaten in darkness (sq. in.).	Area eaten in light (sq. in.).
1	0·97	9·04
2	1·19	7·61
3	3·68	7·39
4	0·91	1·04
5	0·71	4·10
Total	7·46	29·18
Mean/Day/Locust	0·373	1·459

A pattern of alternating chequer-board black and white squares, each 1 cm. square, and a vertical zigzag of stripes were as attractive to the insects as the vertical stripes but a row of six large triangles, each 20 centimetres high and with a base of four centimetres were not so attractive either when upright or inverted. From these trials it will be clear that the grasshoppers were not merely attracted to the contrasting designs.

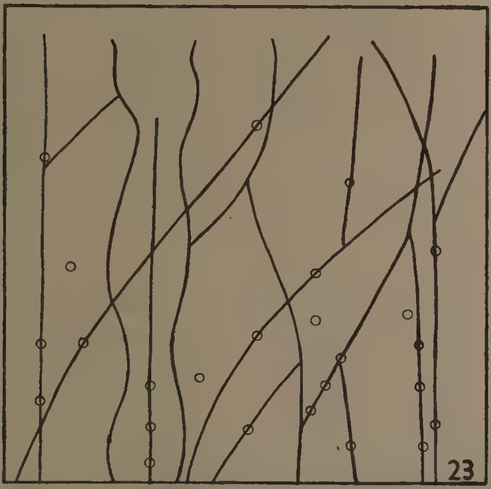


FIG. 23.—Chart obtained in an experiment to show that grasshoppers are attracted to stripes. The positions where the insects rested are marked by circles. Only four individuals out of the twenty-five used in this test did not settle down on or at the edge of a stripe.

TABLE X.—*Experiments to show the attraction of grasshoppers to different patterns.*

(A) Using *Gomphocerippus rufus.*

Expt. No.	Vertical stripes.	White paper.	Total.
1	15	5	20
2	17	3	20
3	18	2	20
Total . .	50	10	60

Expt. No.	Vertical stripes.	Black paper.	Total.
1	14	6	20
2	16	4	20
3	15	5	20
Total . .	45	15	60

Expt. No.	Vertical stripes.	Horizontal stripes.	Total.
1	16	4	20
2	13	7	20
3	14	6	20
Total . .	43	17	60

(B) Using *Chorthippus parallelus.*

Expt. No.	Vertical stripes.	45° stripes	Total.
1	9	11	20
2	12	8	20
3	9	11	20
Total . .	30	30	60

Expt. No.	Vertical stripes.	20° stripes.	Total.
1	13	7	20
2	14	6	20
3	11	9	20
Total . .	38	22	60

Expt. No.	Vertical stripes.	Zigzag.	Total.
1	9	11	20
2	10	10	20
3	12	8	20
Total . .	31	29	60

Expt. No.	Vertical stripes.	Chequer board.	Total.
1	10	10	20
2	9	11	20
3	10	10	20
Total . .	29	31	60

Expt. No.	Vertical stripes.	Upright triangles.	Total.
1	17	3	20
2	16	4	20
3	14	6	20
Total . .	47	13	60

Expt. No.	Vertical stripes.	Inverted Triangles.	Total.
1	17	3	20
2	15	5	20
3	17	3	20
Total . .	49	11	60

It was noticed that the grasshoppers always tended to walk along the edges of the stripes, either when they were vertical or aslant. The same behaviour was seen on the zigzag design where they tried to turn round at the angulations so as to remain in contact with the black pattern. The chequer-board was treated as a simple vertical pattern, for they climbed it vertically by following the left-hand margin of one black square and then the right side of the next square above and so on, in this way always walking up the side of a black square.

No preference was shown for stripes of one width when grasshoppers were tested with a repeated pattern of four different widths of stripes, ranging from 2–18 mm.

Fig. 23 is a copy of a chart which shows how, in an experiment, grasshoppers rested in contact with a stripe. Only four out of twenty-five individuals settled down off the pattern.

In this series of experiments it was frequently noticed that, when climbing the stripes, the insects attempted to feed at the edges of the pattern. Thus it seems that the climbing of a more or less vertical design elicits a biting response.

An abundant supply of grass in both a vertical and a horizontal position was distributed over the floor of a large cage. Twenty-five adults of *Chorthippus albomarginatus* were introduced and for six consecutive days records were made whenever a grasshopper took a meal. Table XI shows the number of grasshoppers which chose to feed on the grass in each position. There was a definite preference for upright grass.

TABLE XI.—*Experiment to test the preference of* Chorthippus albomarginatus *adults for upright or horizontal grass.*

Day.	Number of hours of Expt.	Number of grasshoppers.	Number feeding on grass (a) upright.	(b) horizontal.	Total number of observations.
1	8	25	11	4	15
2	8	25	20	8	28
3	8	25	18	17	35
4	8	25	42	16	58
5	7	25	28	10	38
6	6	25	20	7	27
Total	45	—	139	62	201

(ii) *The antennae and smell.*—Many phytophagous insects have been shown to be attracted to their host plants by a sense of smell. Present opinion is that the antennae are the main olfactory organs but that structures in other parts of the body may serve as subsidiary centres of olfactory perception.

A set of experiments was carried out to observe the effect of amputating the antennae on food consumption (Table VIII). The antenna-less insects did not appear to have been handicapped in their ability to find food.

Fig. 24 is a diagram of an apparatus used to test the sense of smell of Acrididae. The cylindrical chamber was 12 inches high and had a diameter of 7 inches. About 20 first and second stage *Locusta* hoppers were used in each trial. Counts were made of the number of hoppers over each section and on the sides of the chamber at five-minute intervals for thirty minutes. The results are summarised in Table XII.

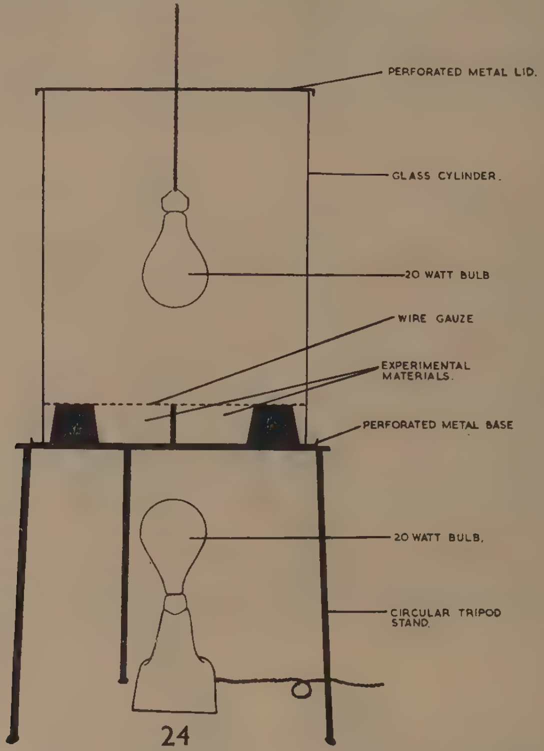

PERFORATED METAL LID.
GLASS CYLINDER.
20 WATT BULB
WIRE GAUZE
EXPERIMENTAL MATERIALS.
PERFORATED METAL BASE
20 WATT BULB.
CIRCULAR TRIPOD STAND.
24

Fig. 24.—Diagram of apparatus used to test the olfactory sense of Acrididae.

Table XII.—*Experiment to test the olfactory sense of* Locusta *hoppers.*

Number of trials.	Number of counts.	Number over green raffia.	Number over *Holcus mollis.*	Number on sides, etc.
12	72	645	649	317
			Number over *Arrhenatherum elatius.*	
10	60	537	513	273
		Number over *Holcus mollis.*		
12	72	561	602	337
		Number over yellow raffia.	Number over green raffia.	
8	48	554	409	213

No preference was shown for the side containing the more suitable food in any combination. (Note that *Arrhenatherum elatius* is a grass which is not freely eaten.)

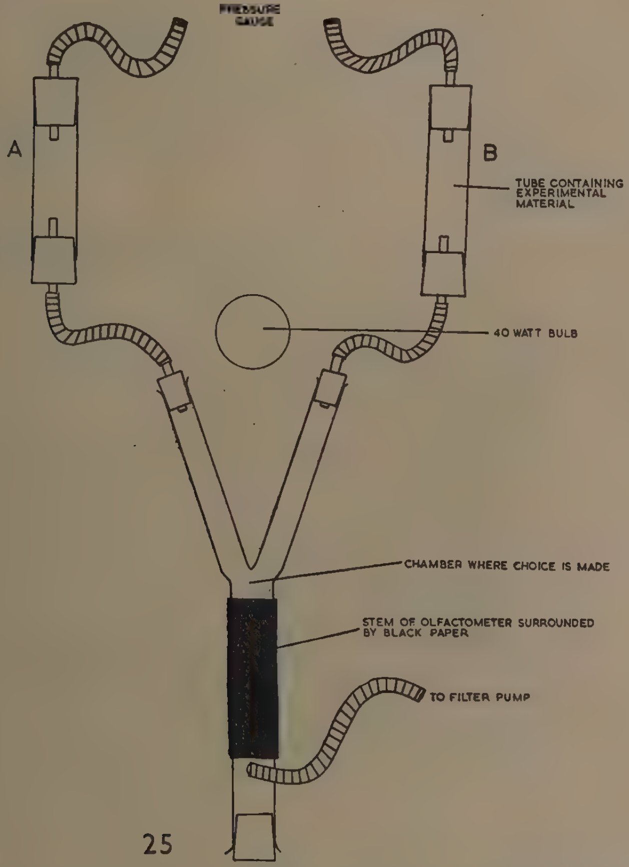

PRESSURE GAUGE
A
B
TUBE CONTAINING EXPERIMENTAL MATERIAL
40 WATT BULB
CHAMBER WHERE CHOICE IS MADE
STEM OF OLFACTOMETER SURROUNDED BY BLACK PAPER
TO FILTER PUMP
25

Fig. 25.—Diagram of Thorpe's olfactometer used in experiments with Acridid hoppers.

Fig. 25 is a diagram of Thorpe's olfactometer which was also used to test the olfactory sense of Acrididae. It was found that the insects passed more rapidly down the apparatus if the stem of the tube was surrounded with black paper to within about an inch of the fork. At the beginning of this work it was noticed that there was a tendency for each hopper to enter the same arm of the olfactometer as that entered by its predecessor. By rinsing out the tube with absolute alcohol after each test this tendency was stopped and the selection of the arms became random. The results are summarised in Table XIII.

Again there is no evidence that an olfactory sense is employed to locate food.

(iii) *The palpi and taste.*—H. and M. Frings (1949) found that in the grasshopper *Melanoplus differentialis*, organs of taste are present at the tips of the maxillary and labial palpi and on the hypopharynx, but nowhere else on the mouth parts or on any other part of the body. A darkening of the cuticle marks the position of these contact chemoreceptors on the palpi.

TABLE XIII.—*Olfactometer experiments with Acridid nymphs.*

Species.	Number in arm leading to cotton wool.	Number in arm leading to *Holcus*.	Total.
Chorthippus parallelus	37	43	80
Locusta migratoria	36	44	80
Schistocerca gregaria	42	38	80

Before feeding grasshoppers bring the tips of their palpi to bear on the surface of the food. Nevertheless, hungry grasshoppers will bite off small pieces of the leaves of plants which they subsequently reject. This suggests that the seat of taste discrimination is in the buccal cavity. However, the tips of the palpi are able to detect the presence of substances in solution (p. 449), so it seems that some chemoreceptors are present on the palpi.

Table VIII shows that amputating the palpi of Locusts does not handicap the insects in finding food.

It has been shown that the grass *Arrhenatherum elatius* is rejected by hoppers of *Locusta* and several British grasshopper species in captivity. By watching the insects it is seen that the plant is only rejected after it has been nibbled at the edge of a blade. The results of experiments to test the palatability of this grass compared with *Holcus mollis* are shown in fig. 1 and 3. Whereas the number of hoppers on *Holcus* increases for 15 minutes, then gradually declines, the number on *Arrhenatherum* decreases from the time of the first count (5 mins.). This is in spite of the fact that, in the first instance, the grasses attract an equal number of insects. Having sampled and rejected *Arrhenatherum*, the grasshoppers move across to the alternative choice.

The rejection of unacceptable plants by grasshoppers was observed both in the field and in the laboratory. In each instance the grasshopper would wander away after first sampling a leaf, often chewing at the next leaf on the same shoot of vegetation. Plants on which these attempts to feed were noted included a species of moss.

Hardness was not the factor concerned here, as was shown by offering the insects the grasses *Dactylis glomerata* and *Bambusa* sp., much tougher species than *Arrhenatherum* but ones on which grasshoppers feed very readily.

An experiment was carried out in which adults of *Chorthippus parallelus* were, in turn, offered green paper, green paper smeared with the grass *Holcus lanatus* and green paper smeared with the leaves of *Digitalis purpurea*. Some coarse sand was used as an abrasive when smearing the plant juices on the paper. Both sides of the paper were treated and it was left overnight to dry. Records were made of the time taken to elicit a biting response, and of the number and duration of the responses made in five minutes. A stop watch was used and a biting response was judged as an opening and closing of the mandibles on the margin of the paper (Table XIV).

The results indicate that the grasshoppers were able to detect the presence of vegetable matter without nibbling but that they were unable to distinguish between the two kinds of prepared paper without an exploratory trial. The response to *Digitalis* paper was less marked than that to *Holcus*.

An investigation was made into the difference in feeding response behaviour between grasshoppers with palpi removed and normal insects. (See Table XV.)

Table XIV.—*Experiment to compare the biting responses of* Chorthippus parallelus *when offered green paper and the same paper treated with the fresh juices of a grass* (Holcus lanatus) *and a herb* (Digitalis purpurea).

	Untreated paper.	Paper treated with *Holcus*.	Paper treated with *Digitalis*.
Number of trials	20	20	20
Number of trials in which a response was observed	0	17	11
Time before first response was noted: 0–1 mins.	.	17	9
Time before first response was noted: 1–2 mins.	.	.	.
Time before first response was noted: 2–4 mins.	.	.	.
Total number of responses observed in a 5 min. period	.	99	31
Mean number of responses/grasshopper	.	5·8	2·8
Range of number of responses	.	1–18	1–6
Total time spent in attempted feeding	.	16 mins. 25 secs.	1 min. 54 secs.
Average time taken in each feed (secs.)	.	9·9	3·7
Range of duration of feeding periods (secs.)	.	2–96	2–17

Table XV.—*A comparison between the feeding response behaviour of adults of* Chorthippus parallelus *with and without palpi. Figures represent time in secs. between commencement of experiment and taking first bite.*

	(A) With palpi.			(B) Palpi amputated.		
Trial.	*Holcus*.	Strips of green paper smeared with *Holcus*.	Strips of green paper.	*Holcus*.	Strips of green paper smeared with *Holcus*.	Strips of green paper.
1	16	28	No response	63	21	52
2	74	14		45	116	72
3	33	9		108	71	81
4	21	13		65	148	64
5	12	38		21	87	47
6	45	12		34	14	175
7	18	24		32	.	.
8	20	17		31	23	65
9	15	10		22	22	60
10	26	42		38	88	132
11	16	26		52	21	.
12	14	23		48	44	67
Total time	310	256	.	559	655	815
Mean	25·8	21·3	.	46·6	59·5	81·5

Grasshoppers without their palpi were slower to make a biting response. No responses were made to green paper by normal grasshoppers, whereas, of the twelve grasshoppers from which the palpi had been removed, ten made a response.

In another experiment it was shown that feeding on the usually unpalatable grass, *Arrhenatherum elatius*, was more prolonged in the case of grasshoppers in which the palpi had been amputated.

The evidence presented in this section strongly suggests that taste is a factor governing the food selection of Acrididae. It also appears that the palpi play some part in taste discrimination although other organs in the buccal cavity are also probably involved. The palpi do not seem to be of any importance in the finding of food.

7. Discussion.

A certain amount of work has been done, especially in North America and Russia, on the range of plants eaten by grasshoppers. Outstanding papers on this aspect are those by Isely (1938) and Criddle (1933) on the North American species and Rubtzov (1932) on the Russian fauna. There is general agreement that the Acrididae are selective feeders, although some species have much wider tastes than others. The Acridinae are, with few exceptions, grass feeders, but the Oedipodinae have more varied tastes and some species feed on broad-leaved plants generally or specifically. The Catantopinae contains a high percentage of herbivorous species. The only previous published work on the food preferences of British Acrididae is that of Clark (1948).

No paper has yet been published which deals with a survey of the factors and aspects of behaviour concerned in the choice of food by grasshoppers. The only worker on the olfactory organs of Orthoptera (*sensu stricto*) is McIndoo (1920), whose views are not generally accepted at the present day. Papers on the olfactory sense of insects of other orders have proved useful in the present investigation, particularly those by Dethier (1937) and Chun Teh Chin (1950). Frings and Frings (1949) worked on the loci of contact chemoreceptors in insects and, although most of their research was on *Periplaneta americana*, they also did some work on other groups, including *Melanoplus* among the Acrididae.

Langford (1930) dealt briefly with certain aspects of grasshopper behaviour but made no study of sense organs.

It appears that the nine British species of Acrididae which have received attention in the food preference section of this work are, under normal conditions, exclusively grass feeders. Most of the British native grasses were found to be freely eaten both by our grasshoppers and by *Locusta migratoria*. *Schistocerca gregaria* is probably a mixed feeder. Numerical experiments showed that some kinds of grass were preferred to others.

A study was made of the physical properties of the food to determine their influence on food selection. Leaf shape, surface texture and depth of colour appear to be of little importance, but toughness and moisture content are probably governing factors. It was found that, when deprived of water as well as of food, grasshoppers would feed on a number of rather succulent plants which are normally left alone. Criddle (1935) drew attention to the fact that certain plants are more readily consumed during hot weather than at other times. It was found that paper was not nibbled when dry, but grasshoppers made persistent attempts to chew it when damp. Leaves of *Holcus mollis* and *Sonchus arvensis* were shown to be eaten less as they dried out. Toughness was shown to influence the feeding of young hoppers of *Locusta* but to have little effect on the habits of the older nymphs and adults.

Toughness and leaf shape were shown to have a considerable effect on the length of time spent in feeding. The grasses with very narrow leaves were more difficult to chew than those with flat ribbon-shaped blades, although they were freely eaten. This must be borne in mind when interpreting the results of numerical food preference experiments. It appears that, when feeding on tough plants, grasshoppers bite off smaller pieces than when eating more tender leaves. This was shown by examining the size of particles in the frass.

A series of laboratory experiments was carried out to determine the senses employed in locating food. A comparison was made between the quantity of food eaten by normal locusts and individuals with either their eyes blackened over, their palpi amputated or their antennae removed. A small quantity of food was provided in a large cage in these trials. The only Locusts which appeared to be handicapped were those with their eyes blackened over and it was subsequently shown that this reduction in the consumption of food was probably due to the insects being less active through the effect of darkness. Locusts kept in the dark consumed less food than those in the light.

Experiments to test olfactory perception also produced negative results and it was concluded that the olfactory sense was of little importance in the locating and selecting of food. However, grasshoppers made no biting response when offered shoots of the Gymnosperm, *Cupressus lawsoniana*, so it is possible that they were able to detect and were repelled by the strongly aromatic resinous oils contained in the tissues of this plant. In nature, a well developed sense of smell is not required by these Acrididae to locate food, as it is always abundant at close hand.

Observations on the feeding behaviour of grasshoppers showed that many plants are nibbled and subsequently rejected as food. This exploratory nibbling was observed on a number of occasions in the field as well as in the laboratory. The moss, *Hypnum cupressiforme*, was twice seen chewed by *Chorthippus parallelus* in the field. Paper on which grass had been smeared, by using coarse sand as an abrasive, was freely nibbled by grasshoppers although untreated paper was left untouched or only slightly chewed. Nibbling of normally unpalatable material was more marked in grasshoppers when their palpi were amputated. These results suggest that the palpi have some function in selecting food although organs in the buccal cavity are possibly also involved. Frings showed that, in grasshoppers, contact chemoreceptors are present at the tips of the palpi and on the hypopharynx. It was found in the present work that a biting response could be elicited in hungry grasshoppers by bringing droplets of sucrose solution of 0·02–0·1 M concentration in contact with the palpal tips.

Observations on the method of feeding employed by grasshoppers showed that leaves in a vertical plane are more easily eaten than those lying flat. Undoubtedly the rosette habit of many plants of chalk pastures makes their leaves difficult to chew whereas the upright blade of a grass is much more easily eaten. An experiment showed that upright blades of grass attract more individuals than similar blades lying flat on the floor of a cage. Grasshoppers resting on grass in the horizontal position often moved to tussocks standing vertically before commencing to feed. Experiments with dark stripes and other patterns on paper showed that grasshoppers are able to appreciate form and are attracted to a pattern of vertical black and white stripes (skototaxis). From these experiments it was concluded that the choice of grasses as food is probably primarily due to the attraction of the grasshoppers to dark upright objects. Probably blades of grass appear to them as vertical dark stripes against a light background of the sky. Thus sight is the important sense used in food locating, but it cannot be the only factor involved as feeding on a reduced scale also takes place in total darkness.

It is thought that after the grasshopper is attracted to the plant by a behaviour mechanism involving skototaxis the biting reflex is elicited. A biting reflex was observed in grasshoppers which had climbed up a black striped pattern. The edge of vertical stripes may be a "sign stimulus" comparable with those described by Tinbergen (1951), which releases the reflex of biting. Attempts to feed on grasses, sedges and rushes are more frequently observed in nature than on herbs and this is probably due to the stimulation of feeding brought about by climbing up the narrow leaf blades of plants of this type.

Once the biting reflex has been initiated other factors begin to operate. Thus, although grasshoppers may be attracted to certain plants because of their form it does not follow that these plants will be freely eaten. Biting and tasting the food which may then be immediately rejected as unacceptable is the normal feeding behaviour of these insects. The indiscriminate nibbling suggests that the sense of smell is poor and the choice of food is mainly governed by taste.

Parts of the plant other than the leaves may be eaten occasionally. The young inflorescences of certain grasses were eaten by grasshoppers both in the laboratory and in the field. Locusts were also induced to feed on the storage organs of some "root" crops.

A study was made of the mandibular morphology and the armature of the crop of the eleven British Acrididae and of the two locust species used in experiments here. The correlation between mandibular morphology and food plants of some American Acrididae was studied by Isely (1944) who showed that, in many species, the mandibles are specially adapted to the type of vegetation which is normally consumed. The crops of only a few species of Acrididae have previously been examined (Chauvin, 1938; Hodge, 1936, 1939; Tietz, 1923). It is interesting, although possibly only a coincidence, that in the two species where the crop armature is most poorly developed, *Oedipoda caerulescens* and *Chorthippus vagans*, the mandibular teeth are most prominent. Study of the mandibular morphology of the types used here suggests that the species which have the best developed mandibles frequent habitats where tough grasses predominate. However, the British Acrididae are a rather uniform group and not very suitable for this kind of work so it is not advisable to generalise from a study limited to so few species.

8. SUMMARY.

1. The British species of Acrididae studied here are normally grass feeders.
2. Some species of grass are preferred to others.
3. The choice of grass eaten depends on the range available.

4. Grasshoppers are able to appreciate form. They are attracted to a number of patterns including vertical stripes.

5. Upright blades of grass are preferred to those lying flat.

6. Leaves in a vertical plane are easier to chew than those which are horizontal.

7. The edge of vertical stripes or blades of grass may serve as a "sign stimulus" which elicits a biting response.

8. There is no evidence that a sense of smell is important in the locating and selecting of food by Acrididae.

9. Taste is probably involved in the selection of food following the initiation of the biting response. From observations, it seems that indiscriminate nibbling and subsequent rejection of many plants is the normal feeding behaviour of Acrididae.

10. Toughness is important, particularly with the young stages.

11. Toughness of food determines the size of particles in the frass.

12. The length of time spent feeding is determined by the toughness and form of the food.

13. Texture appears to be of little importance in the initiation of a biting response.

14. Moisture content is probably a factor determining whether a plant is eaten. Thirsty grasshoppers may feed on succulent plants which are not normally chewed.

15. The intensity of the colour of the food is probably of no importance.

16. Males may spend a slightly longer time than females on individual meals but the latter probably feed at more frequent intervals.

17. More feeding takes place in the light than in darkness.

18. Only a small proportion of the total hours of daylight are spent in feeding.

19. After a meal of grass, the gut is completely emptied of food after about 24 hours, but more than half the frass pellets are voided within the first five hours.

20. The mandibles are adapted to the range of food normally consumed. There are some striking differences in the mandibular morphology even among the small Acridid fauna of Britain.

21. There is considerable variation in the internal armature of the crop. A wide range of variation is found between individuals of the same species, and opposite sides of the crop are often asymmetrical.

22. The British grasshoppers which have been studied in their natural habitats are never found in the absence of grass. Apart from this, the specific composition of the vegetation in the habitat is of little importance in limiting the distribution of the species.

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Vol. 105. Part 19. Pp. 455–474. 15 figs. 22nd December, 1954

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THE HIGHER CLASSIFICATION OF THE FAMILY ISSIDAE (HOMOPTERA : FULGOROIDEA) WITH DESCRIPTIONS OF NEW SPECIES.

By R. G. Fennah, F.R.E.S.

Manuscript received 16th February, 1954.

(Read 5th May, 1954.)

With 15 Text-figures.

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1. Introduction and Historical Résumé.

The classification of Issidae followed by all recent students is based on groupings proposed by Melichar in his *Monographie der Issiden* (1906). On the characters of general body form, relative size of tegmina, presence or absence of a claval suture, and occurrence of foliate protibiae in the male he divided the family into three main groups which he named Caliscelidae, Hemisphaeriidae and Issidae: he then subdivided the last of these, according to degree of wing development, into three lower groups, Hysteropterinae, Issinae and Thioniinae. The higher groups, notwithstanding the terminology used, have never been recognised as families: they have usually been accorded subfamily rank, but where Issidae have themselves been regarded as a subfamily of Fulgoridae they have been relegated to the status of tribes.

This system of dividing the Issidae, which has been in use for nearly half a century, has never been revised or even directly questioned. Baker (1915 : 141) proposed a new subfamily, Augilinae, for the reception of *Augila* Stål and *Augilina* Mel., but *Augila* was correctly removed to Lophopidae by Muir (1930 : 476), where *Augilina* also belongs. A more significant contribution was made by Baker in 1927 (1927 : 406) in the following comment on *Glyphotonga acuminata* Schmidt: " The relationship of the genus appears to be with *Tonga*, and to the Tonginae; apparently here should be referred also *Forculus* Distant, *Forculusoides* Distant, *Orthophana* Melichar, *Paratonga* Schmidt, *Oryxana* Distant and *Hemitonga* Schmidt. They all have one or two subapical teeth on hind tibiae but this character is variable. In more stable characters they appear to be

Issidae.'' (Shortly before this appeared Melichar (1924 : 11) had placed *Orthophana* in the Acanaloniidae). Baker does not appear to have defined his Tonginae, or even to have mentioned such a group elsewhere.

In 1929 Kuznetzov described *Ahomocnemiella*, based on a single species, and for its reception proposed a new subfamily Ahomocnemiellinae, which was described as coming between the Issinae and Eurybrachydinae of Stål. Material of *Ahomocnemiella* examined by the writer in the British Museum was not found to differ in any major character from *Caliscelis* and its allies.

Muir apparently overlooked these last two references, as in his second review of the classification of Fulgoroidea in 1930 he merely presented Melichar's table of subfamilies. Nevertheless, he made two comments (*loc. cit.*) which showed an appreciation of certain weaknesses in the existing classification. "This family (Acanaloniidae) . . . may eventually be sunk into the Issidae, unless other forms are segregated out of Issidae (e.g., *Tonga*) ; but the difficulty at present is to find one or more characters which will characterise such a group.'' "The genus *Ivinga* Distant is interesting and its position not very clear . . . It is best placed in the Issidae.''

During the past few years the writer has taken opportunities to examine material of most of the genera currently placed in the Issidae or Acanaloniidae, and has given particular attention to the shape of the antennae, the proportions of the rostrum, the arrangement of the post-tibial and post-tarsal spines, the structure of the post-tarsus, the form of the female genitalia, and, where possible, that of the male genitalia. As a result it has become evident that Melichar's major groups include two that are natural, though of totally unequal value ("Caliscelidae'' " Hemisphaeriidae '') and one ("Issidae'') that is composed of a heterogeneous assemblage of genera which is not resolved into major natural components by the subgroup characterisation which he gives.

2. SUBFAMILIES.

The data now available disclose the existence of five major natural groups in the family, each of which is here recognised as a subfamily. They are Caliscelinae, Issinae, Acanaloniinae, Tonginae and Trienopinae, and are defined as follows :

Trienopinae subfam. n.

Ocelli absent. Post-tibiae each with two spines laterally ; basal metatarsal joint with more than two spines apically. Tegulae distinct. Tegmina with basal cell small or indistinct, costal margin with a projecting reflected loop basally. Ovipositor with third valvulae long, strongly spinose along short apical margin.

Type genus, *Trienopa* Signoret, 1860, *Ann. Soc. ent. Fr.* (8) **3** : 188.
Type species of genus *Trienopa flavida* Sign., 1860, *loc. cit.*, pl. 5. fig. 4.

Tonginae.

Tonginae Baker, 1927 : 407.

Ocellar scars present. Post-tibiae each with one or two spines laterally ; basal metatarsal joint with more than two spines apically. Tegulae not distinct. Tegmina with basal cell moderately distinct, costal vein distinctly submarginal. Ovipositor with third valvulae minutely denticulate along distal dorsal margin, upper apical margin, and to a slight extent even on external dorsal surface. Aedeagus with a pair of prominent lobes dorsolaterally at base.

Type genus, *Tonga* Kirkaldy, 1900, *Entomologist* **33** : 242.

Type species of genus, *Tonga guttulata* Westwood, 1845, *Arc. Ent.* **2** : 57, fig. 2, 3*a*.

Issinae.

Issites Spinola, 1839, *Ann. Soc. ent. Fr.* **8** : 204.
Issiden Melichar, 1906, *Abh. zool.-bot. Ges. Wien* **3** : 100.

Ocelli present or absent. Mesonotum usually broader than long, never more than 1·5 times as long as broad. Post-tibiae with a variable number of spines, basal metatarsal joint with more than two spines apically. Tegulae not distinct. Tegmina with basal cell obsolete, very feebly demarcated. Third valvulae of ovipositor never furnished with spines and rarely minutely denticulate.

Type genus, *Issus* Fabricius, 1903, *Syst. Rhyng.* : 99.

Type species of genus, *Cercopis coleoptratus* Geoffroy, 1764, *Hist. Ins.* **1** : 418 ; Fabricius, 1775, *Ent. Syst.* **4** : 53.

Acanaloniinae.

Acanonides Amyot and Serville, 1843, *Hist. nat. Ins., Hémipt.* : 58, 520.
Acanaloniidae Stål, 1862, *Handl. Vetensk. Akad., Stockh.* **3** (6) : 68.

Ocelli or ocellar scars present. Rostrum with apical joint longer than broad. Mesonotum usually longer than broad. Post-tibiae almost invariably laterally unarmed, basal metatarsal joint with more than two spines apically. Tegulae narrow, more or less concealed. Tegmina with basal cell usually clearly demarcated, costal vein normally at margin throughout, or margin thickened and flanged below, venation irregularly reticulate. Ovipositor with third valvulae either relatively large, securiform, laterally compressed, with apical margins minutely denticulate along inner surface, or subquadrate with apical margins smooth.

Aedeagus of characteristic pattern as shown in figures below.

Type genus, *Acanalonia* Spinola, 1839, *Ann. Soc. ent. Fr.* **8** : 447.

Type species of genus, *Acanalonia servillei* Spinola, 1839, *ibid* : 448.

Caliscelinae.

Caloscélides Amyot and Serville, 1843, *Hist. nat. Ins., Hémipt.* : 57, 509.
Caliscelidae Melichar, 1906, *Abh. zool.-bot. Ges. Wien* **3** : 3, 4.
Ahomocnemiellinae Kuznetzov, 1929, *Zool. Anz.* **79** : 329.

Ocelli absent. Rostrum with apical joint very short, little, if at all, longer than broad. Mesonotum broader than long. Protibiae occasionally foliate, post-tibiae usually armed laterally with a single spine, basal metatarsal joint with not more than two spines. Tegulae not distinct. Tegmina often brachypterous, occasionally elongate and very narrow, basal cell very small or feebly demarcated. Third valvulae of ovipositor not at all denticulate, strongly rounded.

Type genus, *Caliscelis* Laporte, 1833, *Ann. Soc. ent.* Fr. **2** : 251.

Type species of genus, *Fulgora bonelli* Latreille, 1807, *Gen. Crust. Ins.* **3** : 166.

3. DESCRIPTIONS OF GENERA AND SPECIES.

(i) Subfamily Trienopinae.

Four genera, two of which were placed by Melichar in his group " Issidae ", and one which is described below as new, are referred to this subfamily. *Ivinga*

Distant, notwithstanding its combination of aberrant characters, can be derived so easily from typical *Trienopa* from East Africa and Madagascar, that it cannot justifiably be retained on an equal footing with the other genera, and is accordingly here regarded as a subgenus of *Trienopa*.

Key to Genera of Subfamily Trienopinae.

(1) (2) Vertex not longer than broad, head not produced before eyes for more than length of an eye 3
(2) (1) Vertex longer than broad, head produced before eyes for much more than length of an eye 7
(3) (4) Costal area wide, its cells three times as long as broad **Neotylana** Distant
(4) (3) Costal area very narrow, its cells broader than long 5
(5) (6) Vertex with a transverse carina at apex, margin of wing entire **Trienopa** subg. **Ivinga** Distant
(6) (5) Vertex without a transverse carina at apex, margin of wing trilobate **Trienopa** subg. **Trienopa** Signoret
(7) (8) Genae in side view of head subrectangulate; antennae inserted distad of eyes. Tegmina with clavus extending for two-thirds of total length of tegmen, Sc + R six-branched, M about 14-branched at subapical line . . . . **Togoda** Melichar
(8) (7) Genae in side view of head triangular; antennae inserted below eyes. Tegmina with clavus reaching almost to apex; Sc + R and M with fewer branches at subapical line . . . . . **Ingoma**[1]

Ingoma gen. n.

Vertex quadrate, horizontal, much produced before eyes, lateral margins parallel, anterior and posterior margins truncate; frons narrow, lateral margins feebly diverging distad to clypeus, disc devoid of longitudinal carinae, but traversed near base by a carina which cuts off a quadrate cell; clypeus ecarinate medially, about half as long as frons; ocelli absent. Pronotum with disc longer than broad, anteriorly deeply convex, subtruncate across middle; mesonotum rather shorter than broad. Post-tibiae laterally three-spined, apically eight-spined, basal metatarsal joint seven-spined. Tegmina relatively narrow, costal and apical margins forming a single shallowly convex curve; costal area narrow, sutural angle forming most distad point of tegmen, venation rather sparse adjoining subapical line.

Type species, *Ingoma triquetra* sp. n.

Ingoma triquetra sp. n. (fig. 1, A–D)

Stramineous; frons except distally and near lateral margins, vertex, genae except for a broad oblique band, distal portion of clypeus, both pronotum and mesonotum except in middle line, mesepisternum, coxae, femora except at apex, pro- and mesotibiae at apex, pro- and mesotarsi, and abdominal sclerites suffusedly, fuscous-piceous. Tegmina hyaline, tinged stramineous, veins, a broad fascia overlying submarginal line, and another from Sc at basal third of tegmen obliquely across to Cu, thence to sutural angle, base of clavus slightly and apical half of clavus, fuscous-piceous.

Female: length, 7·0 mm.; tegmen, 5·4 mm.

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[1] Described below.

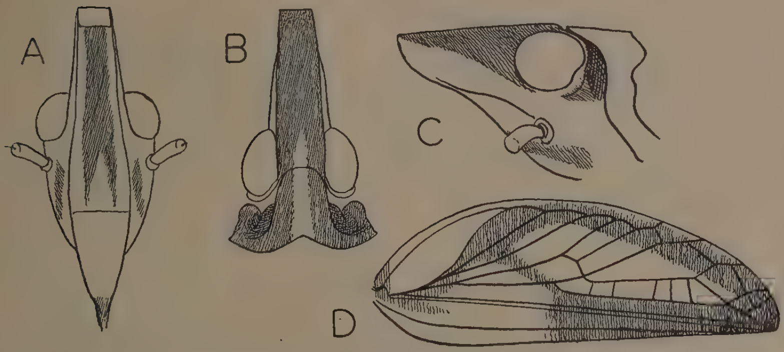

FIG. 1.—*Ingoma triquetra* sp. n. A, frons and clypeus; B, vertex and pronotum; C, head in profile; D, tegmen.

Holotype ♀ KENYA: Kwali forest, 20 miles west of Mombasa, 1.vi.1948 (*Miss M. Steele*) B.M. 1948–347. Type in British Museum (Natural History).

Ingoma is well distinguished by the elongate head, which is not declivous or of the same shape as in *Togoda* Mel., and by the shape of the tegmina. It is here assumed that the spine arrangement on the hind legs is of generic and not merely specific value, but it may prove necessary to modify this interpretation when more data are available.

(ii) Subfamily Tonginae.

The subfamily Tonginae includes twenty genera, separated by the characters given in the following key. The shape of the female genitalia and the basic pattern of the male genitalia are remarkably constant, so much so, indeed, that the latter appear to be of limited value in separating genera. There is a complex of forms centred on *Lollius* Stål which shows much variation in the shape of the head, but less in that of the tegmina. The treatment of this group below has been based principally on use of tegminal characters: this has enabled most existing names to be preserved with only one or two additions. One alternative course, based on the assumed paramountcy of head characters, would have resulted in the erection of numerous monotypic genera. Another course, attractive on account of its apparent taxonomic soundness, would have been to sink all such forms under *Lollius* Stål: the gaps in the available material, however, appear too large to justify such a drastic step. The best course may prove to be the recognition of a number of subgenera of *Lollius*—a treatment virtually the same as that used by Melichar for *Tylana*—but until further material comes to hand the writer prefers to treat genera in this group as being on an equal footing.

Key to Genera of the Subfamily Tonginae.

(1) (2) Apex of clavus terminating in a short but distinct spine[2] . . . (3)
(2) (1) Apex of clavus not terminating in a spine, even if sometimes narrow . . . . (5)

---

[2] See fig. 6H.

(3) (4) Vertex elongate, triangular . . . . **Tonga** Kirkaldy

(4) (3) Vertex subquadrate . . . . **Hemitonga** Schmidt

(5) (6) Tegmina broadest near middle, very strongly tapering distad . (7)

(6) (5) Tegmina quadrate or subtriangular, not strongly tapering distad, frequently widening . . . . (13)

(7) (8) Vertex anteriorly broadly rounded, disc domed transversely, disc of frons ecarinate, hollowed . . . . **Forculus** Distant

(8) (7) Vertex pentagonal or quadrate or head conical in dorsal view . (9)

(9) (10) Vertex strongly produced before eyes, in dorsal view elongate, triangular . . . . **Glyphotonga** Schmidt

(10) (9) Vertex short, quadrate or pentagonal . . . . (11)

(11) (12) Vertex short, pentagonal; tegmina with clavus not reaching apical margin . . . . **Forculusoides** Distant

(12) (11) Vertex quadrate, but margins raised; tegmina apically acute, clavus reaching to apical angle . . . . . . **Orthophana** Melichar

(13) (14) Apex of clavus reaching apical margin of tegmen . . . . . . (15)

(14) (13) Apex of clavus not reaching apical margin of tegmen . . . . (19)

(15) (16) Tegmina distinctly tuberculate between veins . . . . (17)

16) (15) Tegmina not tuberculate between veins, often with veins prominently raised . . . . (23)

(17) (18) Intervenal tuberculation on tegmina very dense; veins almost immersed in corium, apical angle of tegmen obtuse, tegmina widest near middle . . . . **Distiana** Metcalf

(18) (17) Intervenal tuberculation on tegmina not dense; veins distinct, apical angle of tegmen rectangulate, tegmina widest near apex **Andrewsiella** Izzard

(19) (20) Vertex square or broader than long or, if slightly longer than broad, then anterior margin transverse, margins not deeply foliate even if raised; sutural angle of tegmina abruptly subrectangulate or acute . . . . (21)

(20) (19) Vertex longer than broad, margins foliate; sutural angle of tegmina rounded-rectangulate . . . . **Epitonga**[3]

(21) (22) Vertex square or practically so, margins raised; post-tibiae laterally bispinose; frons more than 1·5 times as long as broad, tegmina about 1·5 times as long as broad; species 6 mm. long . . . . **Cotylana**[3]

(22) (21) Vertex much broader than long, margins not raised; post-tibiae laterally unispinose; frons not much longer than broad; tegmina twice as long as broad; species 11 mm. long **Paratonga** Schmidt

(23) (24) Tegmina with apical margin truncate, vertical or practically so, sutural angle subacute or abruptly rectangulate, not rounded . . . . (25)

(24) (23) Tegmina with apical margin convex-truncate, not vertical, sutural angle rounded . . . . (27)

(25) (26) Costal area broad, broader than costal cell, traversed by oblique veins, frons as long as broad . . . . **Oryxana** Distant

(26) (25) Costal area narrow, not broader than costal cell, frons longer than broad . . . . **Capelopterum** Melichar

(27) (28) Clavus in profile sellate, posteriorly vertical, not tapering until very near apex . . . . **Scalabis** Stål

(28) (27) Clavus in profile not sellate, sometimes elevated near base, tapering evenly distally . . . . (29)

---

[3] Described below as new.

(29) (30) Tegmina with twelve to eighteen branches of R and M reaching subapical line . . . . (31)
(30) (29) Tegmina with much fewer branches of R and M at subapical line . (33)
(31) (32) Frons in profile much produced, sub-tricarinate, strongly projected beyond base of clypeus . . . . . . **Paratylana** Distant
(32) (31) Frons only slightly projecting beyond clypeus, tumid, ecarinate; venation swollen as if blistered, veins numerous and parallel **Pseudotylana** Melichar
(33) (34) Tegmina twice as long as broad, vertex angulately produced at middle of anterior margin . . . . **Lollius** Stål
(34) (33) Tegmina much less than twice as long as broad . . . . . . (35)
(35) (36) Vertex broader than long, frons transversely convex, margins not raised, strongly tricarinate . . . . **Issarius** Metcalf
(36) (35) Vertex square, frons flat or transversely triconcave . . . . . (37)
(37) (38) Frons 1·2 times as long as broad, triconcave, with two very distinct carinae and sometimes a feeble median carina **Atylana** Melichar
(38) (37) Frons in middle line 1·3 times as long as broad, flat, very feebly carinate, lateral margins foliately raised, especially at base and side of vertex . . . . **Tylana** Stål

Hemitonga Schmidt.

Hemitonga Schmidt, 1911, *Stettin. ent. Ztg* **72** : 217.
Orthotype, *Hemitonga viridipennis* Schmidt, 1911, *loc. cit.* : 219.

No material of this genus has been examined by the writer. The Bornean type appears to combine the head characters of *Lollius furcifer* Stål with the tegminal characters of *Tylana dyakana* Kirk. (= *T. acutipennis* Mel. (1906 : 200)) also from Borneo. The latter species is provisionally—and with hesitation—referred to *Hemitonga* under the new combination *Hemitonga dyakana* (Kirkaldy).

Distiana Metcalf.

Moniana Distant, 1909, *Ann. Mag. nat. Hist.* (8) **4** : 76. *nom. praeocc.*
Distiana Metcalf, 1952, *J. Wash. Acad. Sci.* **42** : 227.
Orthotype, *Distiana andrewsi* (Kirby).

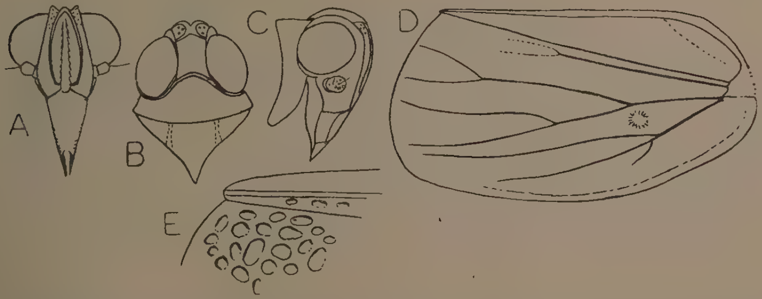

FIG. 2.—*Distiana andrewsi* (Kirby). A, frons and clypeus; B, vertex, pronotum and mesonotum; C, head and pronotum, side view; D, tegmen. E, apex of clavus. (All figures kindly supplied by Dr. W. E. China.)

Distiana andrewsi (Kirby) (fig. 2, A–E).

Kirby, 1900, *Monograph of Christmas Island*: 13, pl. 15.

The writer is indebted to Dr. W. E. China for supplementing his notes on this species, and for providing the illustrations given above of the holotype in the British Museum.

Epitonga gen. n.

Vertex quadrate, longer than broad, margins elevated, frons about 1·1 : 1 times as long as broad, lateral margins diverging to below level of antennae, thence angulately bent mesad to frontoclypeal suture, lateral margins foliate, disc hollowed out, tricarinate, median carina weaker than sublateral carinae, latter not attaining suture, subacutely united basally; clypeus ecarinate, rostrum reaching post-coxae, apical joint as long as subapical. Pronotum about as long as vertex and longer than mesonotum. Post-tibiae laterally two-spined, apically eight or nine-spined, basal metatarsal joint with two large and six minute spines. Tegmina elongately subtriangular, widening to apex, costal margin weakly convex, apical angle strongly rounded, apical margin convex-truncate, sutural angle rounded-rectangulate; corium shallowly hollowed between the prominent veins, C, Sc and R simple to subapical line, M with about 4 branches at subapical line; claval veins united much basad of middle of clavus, clavus very definitely not reaching to apical margin. Wings with R simple or minutely forked at apex, M 2-branched, Cu_1 3-branched.

Type species *Epitonga ferox* sp. n.

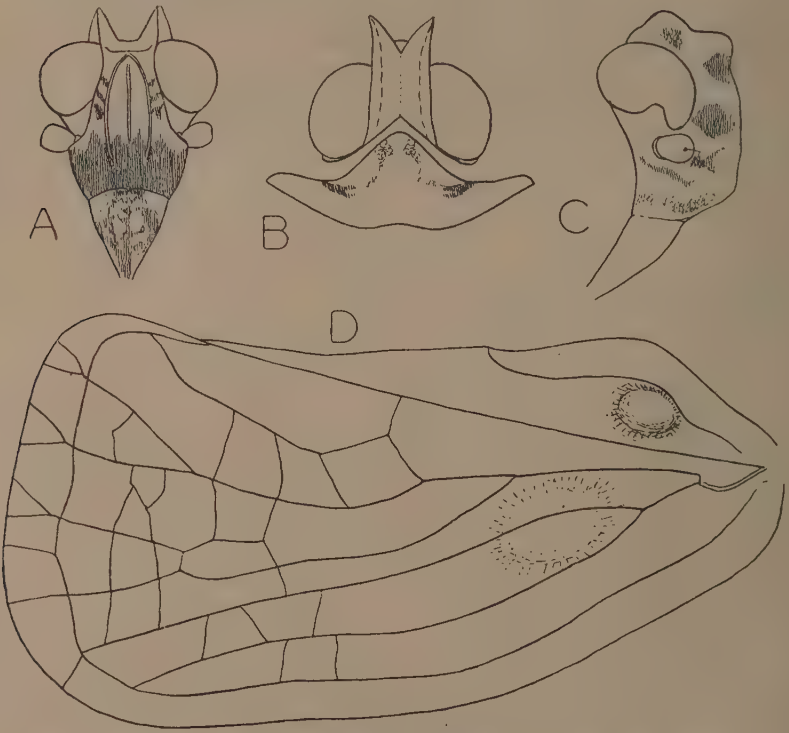

Fig. 3.—*Epitonga ferox* sp. n. A, frons and clypeus; B, vertex and pronotum; C, head in profile; D, tegmen.

Epitonga ferox sp. n. (fig. 3, A–D).

Head in profile subquadrate. Vertex with lateral margins 1·7 times maximum width, lateral margins deeply foliate, anterior and posterior margins angulately excavate ; sublateral carinae of frons meeting dorsally a short distance below anterior margin of vertex, the intervening space medially hollowed ; tegmina with humeral callus and a small callus near base of clavus prominent.

Stramineous ; three obscure bands on frons extending over genae, clypeus, procoxae basally, pronotum behind antennae (except for a short ivory-white bar), mesonotum laterally (except for a raised ivory-white spot), fore and middle legs, post-tibiae, post-femora heavily, sprinkled fuscous-piceous. Tegmina polished, translucent, suffused pale greenish-yellow, a few spots on costal and apical margin and a larger spot between M and Cu at middle of tegmen fuscous-piceous ; transverse veins pallid green.

Female : length, 8·5 mm. ; tegmen, 10·7 mm.

Holotype ♀, SOLOMON IS.: New Georgia, Munda, ii.1945 (*L. A. Conwell*). Holotype in U.S. National Museum.

Cotylana gen. n.

Vertex quadrate, nearly square, anterior margin transverse with an indication of a small triangular projection at middle, lateral margins elevated but not foliate, frons longer than broad (1·6 : 1), lateral margins gradually diverging to below level of antennae then incurved, disc concave, strongly tricarinate with lateral carinae meeting acutely in middle line basally a very short distance before anterior margin of vertex, frontoclypeal suture impressed, rostrum just attaining post-trochanters, apical joint slightly shorter than subapical, ocellar scars present, post-tibiae laterally bispinose, apically 8-spined, basal metatarsal joint ten-spined. Tegmina not twice as long as broad, costal margin convex, deeply rounding into apical margin, sutural angle rectangulate or acute, clavus not reaching as far as apical margin. Wings with R simple for most of length, M and Cu_1 forked at middle, all these veins forked abruptly and subreticulately very close to apical margin, forming an irregular subapical line of veins and with about 12 branchlets reaching margin.

Type species, *Lollius acutipennis* Kirkaldy, 1906, *Bull. Hawaii Sug. Ass. ent. Ser.* **1** (9) : 439.

This concept is separated from *Tylana* by the distinctly tricarinate frons and the relative length of the clavus, which does not reach as far as the apical margin. The number of post-tibial and post-tarsal spines, and the submarginal venation of the wings are as in *Tylana*.

Cotylana acutipennis (Kirkaldy) (fig. 4, F–H).

Lollius acutipennis Kirkaldy, 1906, *loc. cit.*

The figures are of a specimen in the U.S. National Museum.

In addition to the type species, *Lollius angustifrons* (fig. 4, C–E) Kirkaldy (1906 : 439) is placed here. The two species are readily separated by the shape of the sutural angle of the tegmina. *Hemitonga dyakana* (Kirk.) differs from these species in the relative length of the clavus and in size, as well as in basal carination of frons. If it should ultimately prove that this species is in fact close to those of *Cotylana* then it will become a matter of great difficulty to keep genera of the *Lollius* complex apart.

Paratonga Schmidt.

Paratonga Schmidt, 1910, *Stettin. ent. Ztg* **71** : 181. Orthotype, *Paratonga truncaticeps* Schmidt.

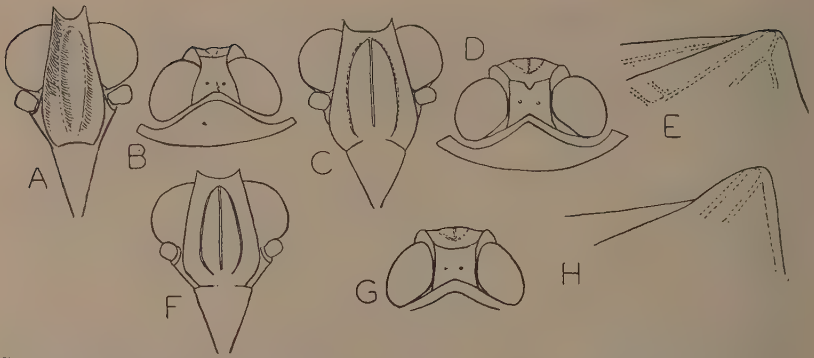

FIG. 4.—*Paratylana herbida* (Wlk.). A, frons and clypeus; B, vertex and pronotum. *Cotylana augustifrons* (Kirk.). C, frons and clypeus; D, vertex and pronotum; E, anal angle of tegmen. *Cotylana acutipennis* (Kirk.). F, frons and clypeus; G, vertex; H, anal angle of tegmen.

Paratonga truncaticeps Schmidt (fig. 5, A–D).

Schmidt 1910, *loc. cit.*: 182.

The figures are of a female specimen from the Fly River, New Guinea, in the British Museum. A female from Mt. Cameron, Tasmania, Aug.–Sept. 1896 (Anthony) coll. Rosenberg is in the collection of the U.S. National Museum.

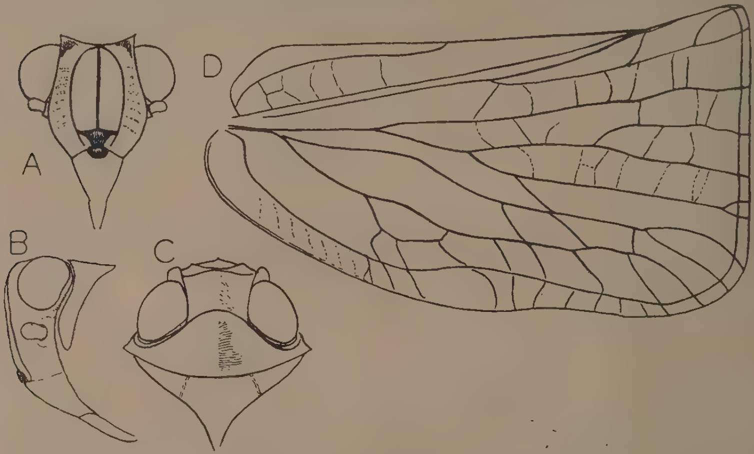

FIG. 5.—*Paratonga truncaticeps* sp. n. A, frons and clypeus; B, head and pronotum in profile; C, vertex, pronotum and mesonotum; D, tegmen.

Capelopterum Melichar.

Capelopterum Melichar, *Abh. zool.-bot. Ges. Wien* **3** (4): 210.

Logotype, *Capelopterum dohrni* Melichar, *loc. cit.*: 211, designated by Schmidt, 1910, *Stettin. ent. Ztg* **71**: 167.

The type species stands apart from all others which Melichar assigned to this genus, and the genus at present must be considered as including only one species. The remainder of those placed here by Melichar appear to belong to *Scalabis*. The specimen figured (fig. 6, C–G) is in the collection of the U.S. National Museum.

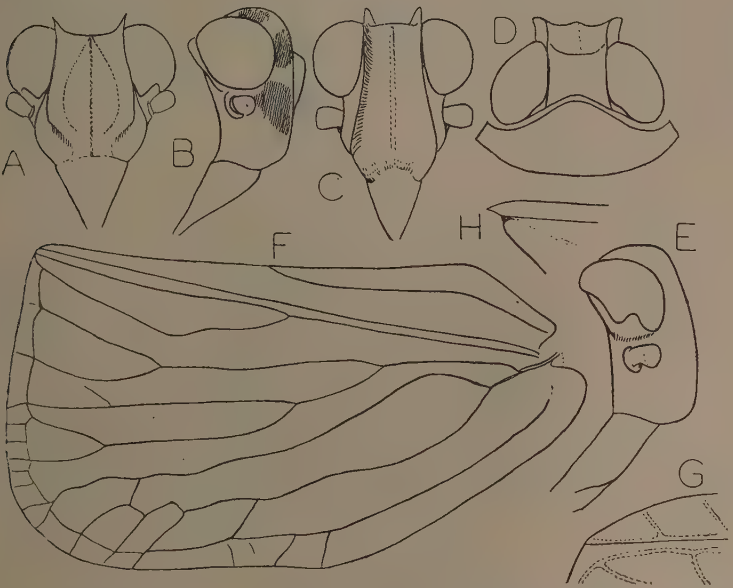

FIG. 6.—*Scalabis hebe* sp. n. A, frons and clypeus; B, head in profile. *Capelopterum dohrni* Mel. C, frons and clypeus; D, vertex and pronotum; E, head in profile; F, tegmen; G, apex of clavus. *Tonga* sp. H, apex of clavus.

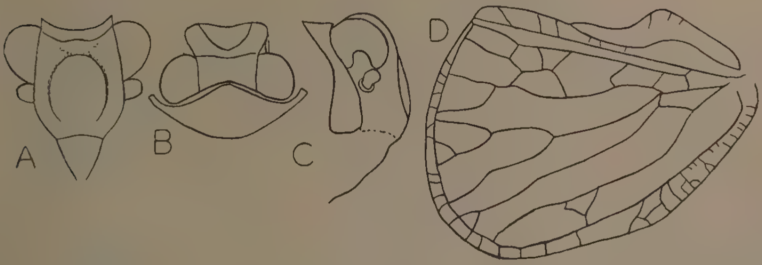

FIG. 7.—*Scalabis philippina* Stål. A, frons and clypeus; B, head and pronotum; C, head and pronotum, side view; D, tegmen.

Scalabis Stål.

Scalabis Stål, 1870, *Öfv. K. Vet. Akad. Förh.* 27 : 762. Logotype, *Tylana* (*Scalabis*) *philippina* Stål.

Scalabis philippina Stål (fig. 7, A–D).

Stål, 1870, *loc. cit.* : 762.

The material seen included the male and female types from the Naturhistoriska Riksmuseum, kindly lent by Dr. René Malaise, and a series in the Baker collection in the U.S. National Museum. Figures were kindly provided by Dr. China of material in the British Museum. Those given here are based on Stål's material. The Fijian species which have been referred to *Capelopterum* (Fennah, 1950, *Bull. Bishop Mus., Honolulu*, **202** : 88–94) are better placed in *Scalabis*.

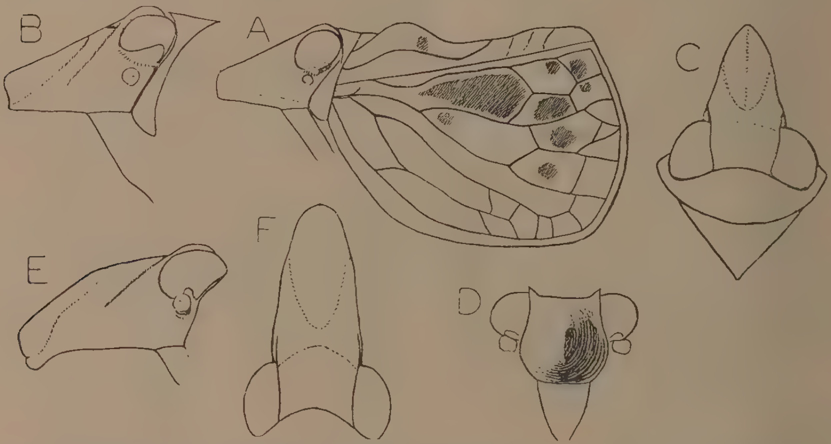

FIG. 8.—*Scalabis nasuta* sp. n. A, side view, legs omitted ; B, head in profile ; C, vertex, pronotum and mesonotum ; D, head, anterior view. *Scalabis nasuta proboscidea* subsp. n. E, head in profile ; F, vertex, dorsal view.

Scalabis nasuta sp. n. (fig. 8, A–D ; 9, A–C).

Vertex broader than long with anterior margin very feebly indicated, frons much produced anteriorly, in profile with its upper half weakly declivous, dorsal and ventral margins converging distally, apical margin weakly sinuate, disc feebly tricarinate or carinae obsolete.

Testaceous ; frons and legs a little darker, clypeus light castaneous. Tegmina testaceous, shining ; intervenal spots of velvety texture in M and Cu distally, russet.

Anal segment of moderate length. Pygofer with laterodorsal angles moderately produced, subangulately rounded. Aedeagus U-shaped, with basal laterodorsal lobes not prominent, sinuate on their upper margin ; distally 3 pairs of spines and a single median spine, all of moderate length, directed dorsad and curved cephalad at tip, the innermost pair also curved mesad ; no processes developed laterally at middle of aedeagus. Genital styles of normal Tongine pattern, as figured.

Male : length, 6·2 mm. ; tegmen, 5·0 mm. *Female :* length, 7·2 mm. ; tegmen, 5·6 mm.

Holotype ♂, allotype and three ♀, PHILIPPINE IS.: Sibuyan Id. (*Baker*).

The head of this species in lateral view is superficially like that of *Paratylana*, but the proportions and carination of the frons are very different. Type in U.S. National Museum.

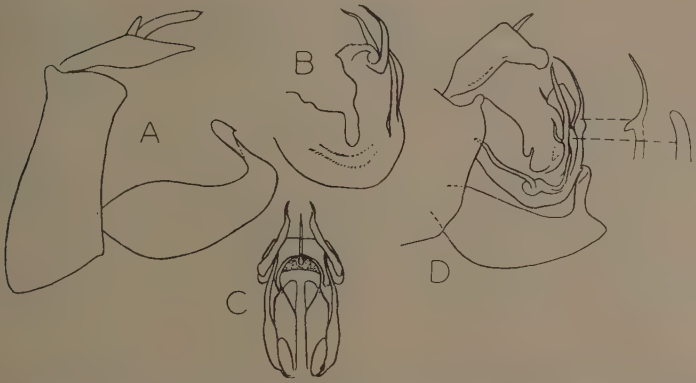

FIG. 9.—*Scalabis nasuta* sp. n. A, anal segment, pygofer and genital style; B, aedeagus, left side; C, aedeagus, posterior view. *Tylana cristata* (F.). D, male genitalia, left side.

Scalabis nasuta proboscidea subsp. n. (fig. 8, E, F).

Frons more produced than in typical subspecies (about 3·5 times the length of an eye), and very distinctly decurved; the pro- and mesotibiae definitely, though not broadly, foliate. Tegmina with apex of clavus relatively more narrowly tapered. Ground coloration fuscous-piceous, tegmina with the veins and their granules distinctly picked out in sordid yellow.

Female: length, 8·0 mm.; tegmen, 6·2 mm.

Holotype ♀ of subspecies from PHILIPPINE IS.: Malinao, Tayabas (*Baker*).

This subspecies is very easily distinguished by the more elongate head. It may prove to represent a new species when a male is examined. Type in U.S. National Museum.

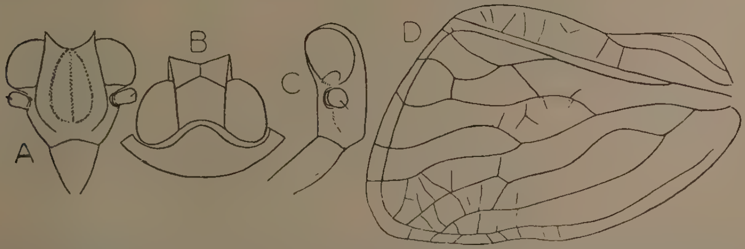

FIG. 10.—*Scalabis juventas* sp. n. A, frons and clypeus; B, vertex and pronotum; C, head in profile; D, tegmen.

Scalabis juventas sp. n. (fig. 10, A–D; fig. 11, A–C).

Frons with median carina more distinct than lateral carinae, but only feebly projecting at base. Clavus in side view as high, two-thirds from base, as height from bottom to top of eye similarly viewed.

Testaceous, sprinkled unevenly fuscous; three spots on head at sides, two indistinct bands on profemora and mesofemora, and three more distinct bands on protibiae and mesotibiae, fuscous. Tegmina greenish-testaceous, translucent, polished, transverse veinlets indistinct, dendroid, greenish-yellow, longitudinal veins reddish-brown interrupted testaceous.

Anal segment of male short, in lateral view with lower margin almost semicircularly lobate in basal half, dorsal and ventral margins distally narrowly tapering. Aedeagus U-shaped in side view, dorsal margin with an unequal pair of vertical lobes on each side near base; lateroventrally a horizontal spinose process attached near its middle; a pair of curved sickle-shaped processes arising laterally near the foregoing pair, curved dorsad and slightly laterad; a second pair of processes distad of these, tapering, shallowly curved, acuminate apically, slightly incurved distally but recurved near apex; distad of these processes a third pair, markedly S-shaped, acuminate at apex. Pygofer and genital styles as figured.

Male: length, 7·1 mm.; tegmen, 9·5 mm.

Holotype ♂, PHILIPPINE IS.: Malinao, Tayahao (*Baker*). Holotype in U.S. National Museum.

To this species are also referred one female from Davao, Mindanao; three females from Zamboanga, Mindanao, and one male from Id. Sibuyan, all taken by Baker. This material differs in the elevation of the lateral carinae of the vertex and in the degree of prominence of the median frontal carina, and probably forms another subspecies. The species is distinguished from others of the genus by the shape of the head, the carination of the frons, the shape of the anal segment of the male and the spinose armature of the aedeagus.

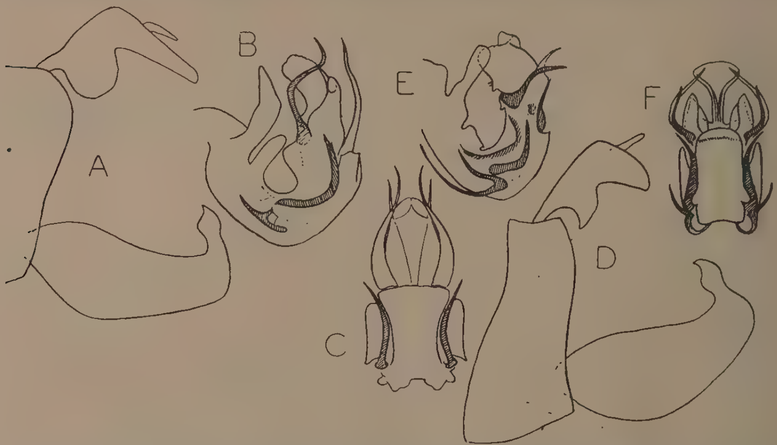

FIG. 11.—*Scalabis juventas* sp. n. A, anal segment, pygofer and genital style, left side; B, aedeagus, left side; C, aedeagus, posterior view. *Scalabis hebe* sp. n. D, anal segment, pygofer and genital style, left side; E, aedeagus, left side; F, aedeagus, posterior view.

Scalabis hebe sp. n. (fig. 6, A, B; fig. 11, D–F).

Frons with median carina distinctly projecting at base.

Testaceous, sprinkled fuscous, sometimes heavily so on frons. Fore and middle legs with femora two-banded and tibiae three-banded. Tegmina sub-translucent, pallid grey, with spots along costal margin and regular interruption along apical margin fuscous ; veins and humeral callus yellowish-brown interrupted with stramineous ; sometimes a brown suffusion over posterior half of corium and middle half of clavus.

Frons, vertex and sides of head of holotype fuscous-piceous ; tegmina with an ivory spot close to base of claval suture and another distally in M, veins distally reddish-brown.

Anal segment of male short, in lateral view with lower margin produced in basal half in a subtriangulate lobe with its apex directed cephalad ; dorsal and ventral margins broadly tapering. Aedeagus U-shaped in side view, dorsal margin with a short, broad subquadrate lobe and a rather long club-like lobe on each side near base ; lateroventrally an asymmetrically U-shaped spinose process lying close against aedeagus and with both limbs directed cephalad ; a pair of short curved spines arising laterally near middle of aedeagus directed caudad then dorsad ; mesad and distad of these a second pair of spines, shorter than the first, directed laterocaudad below aedeagus ; a third pair of spines arising on dorsal surface of aedeagus, each spine sinuately curved round aedeagus to point mesocaudad at apex, apical portion of aedeagus strongly sclerotised, with a pair of short peg-like denticles.

Pygofer and genital styles as figured.

Male : length, 6·8 mm. ; tegmen, 8·4 mm.

Holotype ♂ and one ♂, PHILIPPINE Is. Mindanao : Colobato (*Taylor*). Holotype in U.S. National Museum.

This species differs from the preceding in details of head structure as figured, in the shape of the anal segment of the male and in the spinose armature of the aedeagus.

Paratylana Distant.

Paratylana Distant, 1909, *Ann. Mag. nat. Hist.* (8) **4** : 78. Orthotype, *Issus herbidus* Walker.

Paratylana herbida (Walker) (fig. 4, A–B).

Issus herbidus Walker, 1868, *J. Linn. Soc. Lond.* (*Zool.*) **10** : 121.

The characteristic features of this member of the *Tylana* complex are the elongate tricarinate head and the dense longitudinal distal venation of the tegmina. The figures are of a specimen in the U.S. National Museum.

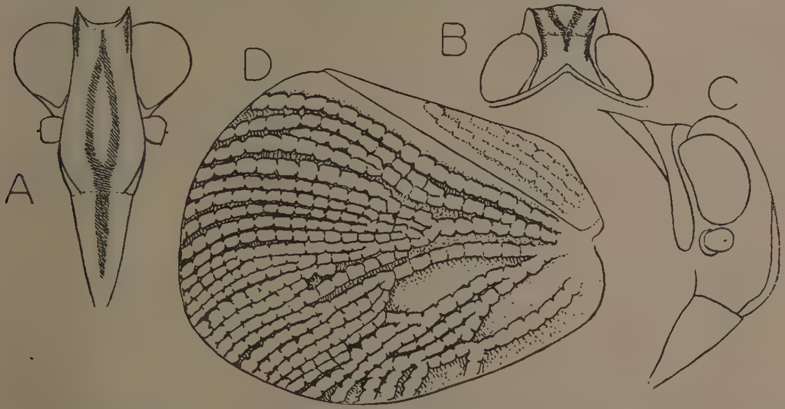

FIG. 12.—*Pseudotylana insculpta* Mel. A, frons and clypeus ; B, vertex ; C, head and thorax in profile ; D, tegmen.

Pseudotylana Melichar.

Pseudotylana Melichar, 1906, *Abh. zool.-bot. Ges. Wien* (4) **3** : 198. Logotype by present designation, *Pseudotylana insculpta* Mel.

Pseudotylana insculpta Melichar (fig. 12, A–D).

Melichar, 1906, *loc. cit.* : 208.

Atylana Melichar.

Atylana Melichar, 1906, *Abh. zool.-bot. Ges. Wien* (4) **3** : 198. Logotype, *Atylana intrusa* Mel., *loc. cit.* : 207.

Melichar gives " Stirne mit zwei Kielen " as the characteristic of *Atylana*, but the median carina is sometimes weakly present.

Lollius Stål.

Lollius Stål, 1866, *Hemiptera Africana*, **4** : 209. Orthotype, *Lollius australicus* Stål.

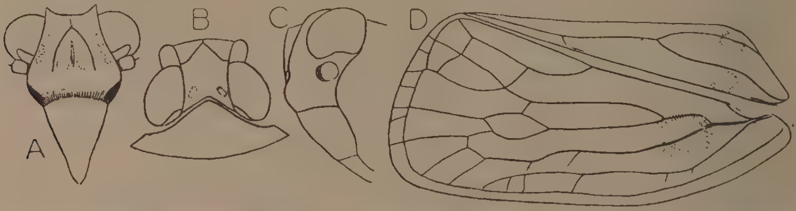

Fig. 13.—*Lollius australicus* Stål. A, frons and clypeus; B, vertex and pronotum; C, head, side view; D, tegmen.

Lollius australicus Stål (fig. 13, A–D).

Stål, 1870, *Öfv. K. Sven. Vet. Akad., Förh.* **27** : 763.

The figures are of a female from a series of two males and four females from Bribies Id., near Brisbane, Australia, January 1925, in the U.S. National Museum.

Lollius is well represented from Australia to the Philippines, and examination of male genitalia has shown beyond doubt that several distinct species are involved. In external characters they differ in relatively minor details from the type species, and the limited extent of their variation strongly suggests that in this group of Issidae the natural species groups are compact and distinct, even if not by a very wide margin.

Tylana Stål.

Tylana Stål, 1862, *Rio Jan. Hemipt.* **2** : 67. Logotype, *Issus cristatus* F. designated by Schmidt 1910, *Stettin. ent. Ztg* **71** : 165.

Tylana cristata (Fabricius) (fig. 9, D; 14, A–E).

Issus cristatus Fabricius, 1803, *Syst. Rhyng.* **2** : 100.

The figures are of a specimen from Réunion (Ile Bourbon) in the collection of the U.S. National Museum. Unless the broad interpretation of this genus used by Stål and Melichar is followed, *Tylana* must at present be considered as including only *cristata* Fab. and *carinata* Fab. (if these are two species). *Tylana ustulipunctata* Uhl. belongs in *Thionia* Stål.

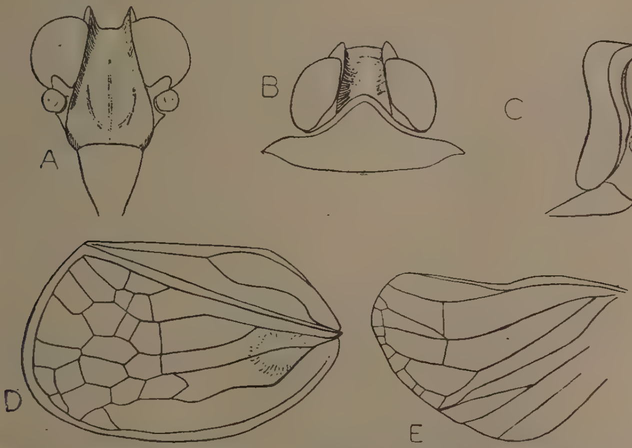

FIG. 14.—*Tylana cristata* (F.). A, frons and clypeus; B, vertex and pronotum; C, head and pronotum, side view; D, tegmen; E, wing.

(iii) Subfamily Acanaloniinae.

The characters which have served in the past to define the group at family level (Melichar, 1924; Muir 1925, 1930) comprise the following: posterior margin of pronotum shallowly concave, mesonotum large and long, post-tibiae devoid of spines, tegmina steeply tectiform, devoid of a precostal area and with venation reticulate.

These characters in combination do not apply to all the genera here recognised as natural members of the group. In *Euthiscia tuberculata* V. D. the hind margin of the pronotum and the proportions of the mesonotum, and its size relative to the rest of the body, are as in many Issine genera (e.g., *Thionia*): laterally unarmed post-tibiae occur in species of the Issine *Colpoptera*, while steeply tectiform tegmina are not rare in Issinae (e.g., *Ugoa*). In *Euthiscia* the costal vein is distinctly submarginal, and is distally connected to the margin by a few cross veinlets: in Issinae the costa is usually marginal, but sometimes submarginal, while in some species of *Pterilia* the precostal area which is developed is relatively as large as that found anywhere in Fulgoroidea. Reticulate venation of the tegmina occurs widely in Issinae. The green coloration so commonly found in Acanaloniinae is not taxonomically characteristic: green forms are common in Issinae (e.g., *Ugoa glauca*, *Issarius* spp.), while in *Euthiscia* one species is pallid testaceous and another is mottled dark brown.

On the characterisation hitherto accepted there is no place at which a dividing line can be drawn to separate off the Acanaloniine group. The form of the ovipositor is of considerable interest, and shows at once that the New World group is a natural unit quite distinct from the Old World group. The case for the two groups being of common origin is not yet proven, but the evidence so far available from the structure of the male genitalia supports the view that the group is a natural one. The feature which appears so far to be characteristic of Acanaloniinae is the occurrence in the aedeagus of two pairs of processes directed caudad, the shorter underlying the longer. But the gap between typical Issinae and *Acanalonia* is very nearly bridged by the condition in *Euthiscia tuberculata* V. D. and *E. signata* V. D. (which were placed by Van Duzee and Doering in Issidae), and accordingly, in the absence of any abrupt change between Issinae, *Euthiscia* and *Acanalonia*, it is scarcely justifiable to regard *Acanalonia* and its allies as constituting a separate family and as more fundamentally distinct than Tonginae or Trienopinae.

Key to Genera of Subfamily Acanaloniinae.

(1) (2) Post-tibiae with six to eight spines at apex ; lateral margins of pronotum not carinate. Ovipositor with third valvulae minutely denticulate along distal margin. New World . . (3)

(2) (1) Post-tibiae with less than six spines at apex ; lateral margins of pronotum more or less distinctly carinate. Ovipositor with third valvulae not at all denticulate. Old World . . . (9)

(3) (4) Tegmina very distinctly widest at one third from base ; claval suture reaching to apical margin . . . . (5)

(4) (3) Tegmina widest at or distad of middle ; claval suture not reaching apical margin . . . . (7)

(5) (6) Lateral margins of frons produced laterad ; tegmina with costal vein at margin ; second post-tarsal joint with a spine at each side and three small teeth on distal margin **Galapagosana** Distant

(6) (5) Lateral margins of frons produced antero-laterally, costa distinctly submarginal, second post-tarsal joint with a spine on each side and a row of eight small teeth along distal margin **Euthiscia** Van Duzee

(7) (8) Tegmina widest at middle, vertex twice as long as broad, genae angulately produced . . . . **Thiscia** Stål

(8) (7) Tegmina widest distad of middle, vertex relatively shorter, genae not produced laterad . . . . **Acanalonia** Spinola

(9) (10) Vertex, pronotum and mesonotum convex ; vertex or pronotum with a fine median line or distant longitudinal carina . . . (11)

(10) (9) Vertex, disc of pronotum and disc of mesonotum flat, not at all convex, vertex and pronotum not obviously carinate in middle ; disc of frons twice as long as broad, slightly narrowed towards clypeus and towards basal margin, with a prominent median carina throughout . . . . **Hemithiscia** Schmidt

(11) (12) Frons convex throughout, devoid of long setae . . . . (13)

(12) (11) Frons in middle with a shallow longitudinal impression, broadening towards the clypeus, and a distinct median carina from basal margin to slightly distad of middle, disc rather sparsely beset with long hair-like setae . . . . **Pseudothiscia** Schmidt

(13) (14) Frons strongly convex with three longitudinal carinae, the median more distinct than the lateral . . . **Parathiscia** Melichar

(14) (13) Frons with a fine median carina only . . . **Paraphilatis** Melichar

Euthiscia Van Duzee.

Euthiscia Van Duzee, 1923, *Proc. Calif. Acad. Sci.* 12 : 193. Orthotype, *Euthiscia signata* Van Duzee.

Euthiscia signata Van Duzee (fig. 15, A–D).

Van Duzee, 1923. *loc. cit.* : 193.

The short lateral appendages of the aedeagus are the counterpart of the latero-ventral appendages in *Acanalonia*. The figures are of a specimen in the U.S. National Museum.

The genus *Galapagosana* Distant is extremely close to *Euthiscia*, and must be referred to Acanaloniinae. In *Galapagosana* the lateral margins of the frons are strongly produced laterad, the costa in the tegmina is marginal, and the second post-tarsal joint has a spine at each side and three small teeth along the distal margin, while in *Euthiscia* the lateral margins of the frons are produced anterolaterally, the costa is distinctly submarginal, and the second post-tarsal joint bears, in addition to the two latero-apical spines, an even row of about eight small teeth along the distal margin.

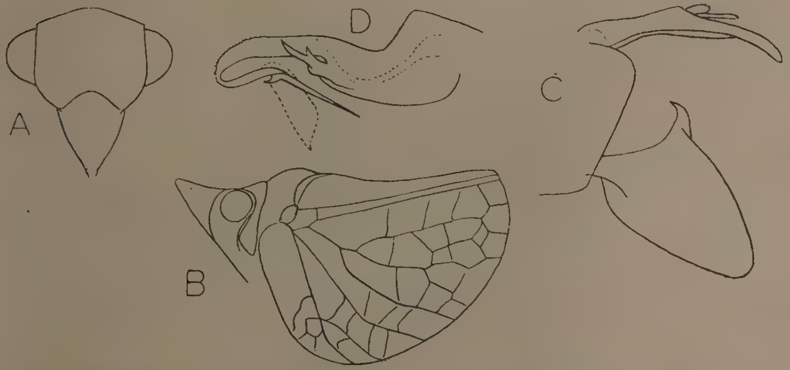

FIG. 15.—*Euthiscia signata* Van Duzee. A, frons and clypeus; B, lateral view, legs omitted; C, posterior margin of pygofer, anal segment and genital style, left side; D, aedeagus, right side.

Hemithiscia Schmidt.

Schmidt, 1912, *Stettin. ent. Ztg* 73 : 95. Orthotype, *Hemithiscia taeniatifrons* Schmidt. *loc. cit.*

Thinea Melichar, 1912, *Ergebn. zweite dtsch. zentr. Afr. Exped.* 1 : 130. Haplotype, *Thinea devota* Mel., *loc. cit.*

The writer has examined African material which agrees satisfactorily with the definitions of both the above genera, and considers that they are better regarded as synonymous.

Consideration of the subfamilies Caliscelinae and Issinae is left for a further report : the former of these groups appears to present no taxonomic problem above generic level, whereas the latter presents so many that separate treatment is advisable.

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23 DEC 1954
Eu. 344

Vol. 105. Part 20. Pp. 475–491. 8 figs. 22nd December, 1954

THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

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PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

Price 6s. 0d.

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KEYS TO THE DESCRIBED SPECIES OF NEW ZEALAND PSYCHODIDAE WITH DESCRIPTIONS OF EIGHT NEW SPECIES.

By G. H. Satchell, Ph.D., F.R.E.S.
(The Museum, Dunedin, New Zealand.)

Manuscript received 10th December, 1953.
(Read 6th May, 1954.)

With 8 Text-Figures.

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Introduction.

Since the publication of my first account of the New Zealand Psychodidae (1950), material of a further five new species has been collected from around Dunedin. In addition, specimens of a new species of *Pericoma* Walker have been loaned me by Mr. E. G. Turbott of the Auckland Museum, and a further two undescribed species of this genus were present in the Tonnoir collection. These eight new species will be described in this paper.

In my 1950 paper I omitted to provide a key to the species and I am, therefore, including one at the beginning of this paper; it covers all the forty-three species known to occur in the Dominion. In addition to the species occurring on the two main islands of New Zealand, I have extended the key to include *Psychoda acutipennis* Tonnoir from Bounty and Antipodes Islands, south of New Zealand. The keys are primarily designed to cover male specimens, but the generic and more than half of the specific diagnoses are applicable to both sexes. The points at which the keys become restricted to the male sex are obvious, as the criteria of separation there concern features of the male genitalia only. This limitation is inevitable as so many of the sibling species are either not satisfactorily separable in the female sex, or the female is unknown. In spite of this limitation, I think the keys will be generally useful because, particularly in the genus *Psychoda* Latreille, the most commonly taken species are also the most readily distinguishable ones, being characterised by colour characters present in both sexes. Caution is necessary however, in identifying the uniformly greyish species of *Psychoda* because, in all probability, only a fraction of the species have been described, and even these can only be identified when good preparations of the male genitalia are available.

Since the publication of my 1950 paper, one described species not mentioned there has been recorded from New Zealand. This is *P. pseudoalternata* Williams, an Australian species also recorded from Hawaii; I have given a full description of it in a paper on the Australian Psychodidae (Satchell, 1953).

The material used in drawing up the descriptions of the eight new species will be deposited in the Tonnoir collection, at the Cawthron Institute, Nelson. Unless otherwise stated the specimens were taken by myself.

KEY TO GENERA.

1. Flagellar segments of antenna fusiform, without a definite neck . . 2.
   Flagellar segments of antenna with a swollen basal bulb and a narrow apical neck . . . . 5.
2. Rs 3-branched, i.e., only one vein intervening between the two forks . 3.
   Rs 4-branched, i.e., two veins intervening between the two forks . . 4.
3. Cu long, reaching beyond level of medial fork . . **Trichomyia** Haliday
   Cu short, scarcely reaching to level of origin of Rs . . **Sycorax** Haliday
4. Cu less than half as long as M_4 . . . . **Nemopalpus** Macquart
   Cu more than half as long as M_4 . . . . **Pericoma** Walker
5. Last one to three antennal segments diminutive and lacking necks. Wing with hairs on veins only . . . . **Psychoda** Latreille
   Terminal antennal segments not diminutive; all flagellar segments with necks. Wing with hairs on veins and membrane . **Brunettia** Annandale

KEYS TO SPECIES.

Trichomyia Haliday.

One described species, *T. fusca* Sat. (Satchell, 1950 : 148).

Sycorax Haliday.

1. R_3 distinctly longer than stem of radial fork . . . . 2.
   R_3 equal to, or shorter than stem of radial fork . . . . 3.
2. Male with bifid aedeagus with inrolled lateral margins toothed **impatiens** Sat. (Satchell 1950 : 150).
   Male with bifid aedeagus consisting of two simple unrolled processes **cryptella** Sat. (Satchell 1950 : 149).
3. Male with cercopod ending in a heavily sclerotized heeled lobe; aedeagus subcylindrical, four times as long as broad **dispar** Sat. (Satchell 1950 : 150).
   Male with cercopod terminating in a ventral semicircular lobe and a dorsal process, not heel-like; aedeagus subcylindrical and scarcely twice as long as broad . . . . . **milleri** Sat. (Satchell 1950 : 151).

Nemopalpus Macquart.

One described species: *N. zelandiae* Alexander, 1921; Tonnoir 1922, 1940, (as *zealandicus*).

Pericoma Walker.

1 Large blackish or brown species, wings 3·5–4 mm. long; Sc joined to R_1 apically; white markings on wings . . . . . . 2.

Smaller brown, patterned or yellow species, wings 2–3 mm. long; Sc not joined to R_1 . . . . . . 3.

2. A white tuft at the wing margin, behind each vein tip, those on the posterior margin overlying the fringe; thoracic display organ in male above anterior spiracle . . **funebris** Hutton (Satchell 1950 : 152).

White tufts on disc but not at vein tips; no display organ in male **multimaculata** Sat. (Satchell, 1950 : 153).

3. First basal cell considerably longer than second; small brownish species with wings either mottled with patches of white and dark brown hair, or uniformly brown . . . . . . 4.

Basal cells equal or almost so; mainly uniformly golden-yellow species; occasionally some infuscation on wing . . . . . . 9.

4. Origin of stem of radial fork much before apex of first basal cell; a large whitish-brown species with two prominent white spots in the wing disc . . . . . . **clarkei** sp. n.

Origin of stem of radial fork at or after apex of first basal cell . . 5.

5. R_3 proceeding inwards from wing margin and ending blindly, not turning upwards to join R_2; medial fork complete; aedeagus of one curved element which is a continuation of the main piece, and one almost straight separate piece beside it . . . . **solitaria** sp. n.

R_3 bending upwards to form a fork with R_2; medial fork complete; aedeagus otherwise . . . . . . 6.

6. Aedeagus composed of three well sclerotized elements, the centre one twice as long as the others, projecting posteriorly as a straight rod **claviata** Sat. (Satchell, 1950 : 156).

Aedeagus with no one element more than one-third as long as the next longest . . . . . . 7.

7. Male style with distal third bent outwards so that inner margin of style is curved convexly near apex; aedeagus of two main and two lateral pieces, making a group of four **maura** Sat. (Satchell, 1950 : 157).

Male style with distal third either straight or bent inwards, so that inner margin is either straight or curved concavely near apex . . . . 8.

8. Aedeagus with the two well sclerotised central elements both slightly curved in the same direction; an unsclerotised element to one side ends in three claws, but is only visible in stained preparations; a very contrastedly coloured species with brown tufts on the wings **triuncinata** Sat. (Satchell, 1950 : 154).

Aedeagus with two-pointed, much curved elements, arranged with the concave surfaces facing, like a pair of calipers; an inconspicuously marked or unicolorous species **drepanata** Sat. (Satchell, 1950 : 156).

9. Uniformly golden-yellow species with at most a faint brownish infuscation on the anterior and posterior fringes, visible only in certain lights . . . . . . 10.

Golden-brown species with the wing infuscated in the distal portion . 15.

10. Coxites without infrabasal processes in male . . . . . . 11.

Coxites with infrabasal processes in male . . . . . . 12.

11. Aedeagus of two slightly curved pointed elements, attached proximally to membranous lobes . . . . **lobisterna** Sat. (Satchell, 1950 : 158).

Aedeagus of two bluntly-ending oblong elements with a filamentous pointed element between . . . **gourlayi** Sat. (Satchell, 1950 : 160).

12. Aedeagus of two curved sickle-shaped elements; anal flap sharply pointed at tip . . . . **bifalcata** Sat. (Satchell, 1950 : 159).
Aedeagus of 3 or 4 elements, one much longer than the others; anal flap bluntly rounded at tip . . . . 13.

13. Long angulated element of aedeagus narrowing to tip and not toothed. 14.
Long angulated element broadening to tip where it ends in a number of pointed teeth . . . . **barbata** sp. n.

14. Long element of aedeagus not obviously right angled but loosely bent through almost a complete circle; infrabasal processes not projecting beyond inner margins of coxites, when seen in dorsal view . . . . **spiralifera** Sat. (Satchell, 1950 : 161).
Long element of aedeagus bent through two right-angled bends; infrabasal processes projecting beyond inner margins of coxites **bilobata** sp. n.

15. Pale golden-brown species with the wings infuscated in the distal third and a white patch in the wing fringe extending from tip of R_2 to M_2 . . . . **serratipenis** Sat. (Satchell, 1950 : 162).
Pale golden-brown species with a transverse brown fascia at level of tips of M_3–M_4 and another above basal cells; no white space in wing fringe . . (= **furcata** Satchell, 1950 : 163, nec Kinkaid, 1899) **diffusa** nom. n.

Psychoda Latreille.

1. Eye bridges well-developed, not separated by a width greater than 5 facets. Wings normal . . . . 2.
Eye bridges narrowed, separated by a width of 10 facets or more; wings shortened and narrowed, veins pushed together **acutipennis** Tonnoir (Satchell, 1950*a* : 42).

2. Antennae 16 segmented, the last three segments diminutive . . . 6.
Antennae 14, or 15 segmented . . . . 3.

3. Antennae 14 segmented; parthenogenetic, females only **severini** Tonnoir sub sp. **parthenogenetica** Tonnoir
Antennae 15 segmented . . . . 4.

4. A whitish species with a dark transverse zig-zag fascia across the wing; segment 14 of antenna very small and naked, separated from thirteenth . . . . **spatulata** Sat. (Satchell, 1950 : 166).
Yellowish-brown species with black spots at vein tips; fourteenth segment of antenna not naked, partially fused with thirteenth . . 5.

5. Male style sinuate when seen in profile; female with Y-shaped subgenital plate . . . . **alternata** Say
Male style evenly tapered and curved when seen in profile; female with subgenital plate replaced by a tubular process **pseudoalternata** Williams (Satchell, 1953).

6. Last three antennal segments subspherical, well separated . . . . 7.
Segments 13, 14 and 15 with no trace of a neck between; sensory cones on 13 and 15; female with an elongate fish-tail shaped subgenital plate . . . . **harrisi** Sat. (Satchell, 1950 : 171).

7. Wings patterned or marked . . . . 8.
Wings uniformly greyish-ochraceous, occasionally yellowish or brown . . . . 11.

8. Yellowish species with basal fifth of wings blackened; blackish legs with white tarsi . . . . **philpotti** Sat. (Satchell, 1950 : 175).
Wing patterned in some other way . . . . 9.

9. Wing disc uniformly greyish; fringe with two creamy-white spaces, one at tip of M_3 and a larger one at tip of Cu . . . **pulchrima** sp. n.

Wing disc patterned, as well as fringe . . . . 10.

10. Wings blackish-brown with two rows of white tufts, one at level of tip of R_2, and one at level of radial fork; white space in fringe at apex and at tip of M_3 . . . . . . **setistyla** Sat. (Satchell, 1950 : 169).

A yellowish-white species with brown wings banded with white forming three fasciae, one at base, one at level of radial fork, and one from tip of R_2 almost to apex . **zonata** Sat. (Satchell, 1950 : 167).

11. Male with a sharply delimited pencil of squamose hairs lying under wing, borne on a reflected costal flap; ninth sternite with lateral margins prolonged posteriorly; abdomen with tufts of squamose hairs. Female with subgenital plate of characteristic shape . . . . **penicillata** Sat. (Satchell, 1950 : 176).

No pencil of hairs under wing in male . . . . 12.

12. Thorax of male covered with a vestiture of short curled scales; aedeagus starting as a single piece, bifurcating near tip; paired pilose lobes present beneath aedeagus . **squamulata** Sat. (Satchell, 1950 : 174).

Male thoracic vestiture mainly hairy . . . . 13.

13. Yellowish species with lanceolate wings; male style long and almost straight, aedeagus of one long straight medial element and one curved lateral element widely separated from it; a median ventral rounded lobe present beneath aedeagus . . . . . . **formosa** sp. n.

Predominantly greyish species . . . . 14.

14. Antennae very long, almost three times as long as wing width in both sexes; aedeagus complex, consisting of four rod-like elements of almost equal length . . . **inaequalis** Sat. (Satchell, 1950 : 174).

Antennae never more than twice as long as wing width, usually less; aedeagus composed of less than four elements . . . . 15.

15. Aedeagus apparently consisting of a single median element, though showing signs of a median split; paired, widely separated, median ventral pilose lobes present below aedeagus . . . . . **simplex** sp. n.

Aedeagus consisting of two elements, a median piece usually with a rounded end, and an angulated piece lying across it, with a pointed end . . . . 16.

16. Cercopods (excluding retinaculum) short, much swollen basally, scarcely longer than style; median ventral lobe with a straight truncated posterior margin; aedeagus with two elements enclosed one within the other to give the appearance of a single tapering process . . . . **cinerea** Banks

Cercopods always at least half as long again as style . . . . 17.

17. Style with three short needle-like setae inserted in a row down the internal side; no median ventral pilose lobe below aedeagus
triaciculata Sat. (Satchell 1950 : 172).

Style with scattered setae arranged otherwise; median pilose lobe present below aedeagus . . . . 18.

18. Median element of aedeagus bearing a fine, pointed process arising from its lateral margin, so that three elements appear to be present
tridens sp. n.

Median element of aedeagus undivided . . . . 19.

19. Styles a little longer than coxites, slender, gently tapering, only slightly curved, with a prominent preapical seta of moderate length, and a long seta near the base in addition to the usual small scattered setae . . . . **novae-zealandicae** Sat. (Satchell, 1950 : 170).

Styles subequal to coxites, curved, with a single long seta at the base, and no significantly longer one near the tip **lloydi** Sat. (Satchell, 1950 : 172).

Brunettia Annandale.

One described species, *B. novae-zealandica* Sat. (Satchell, 1950 : 165).

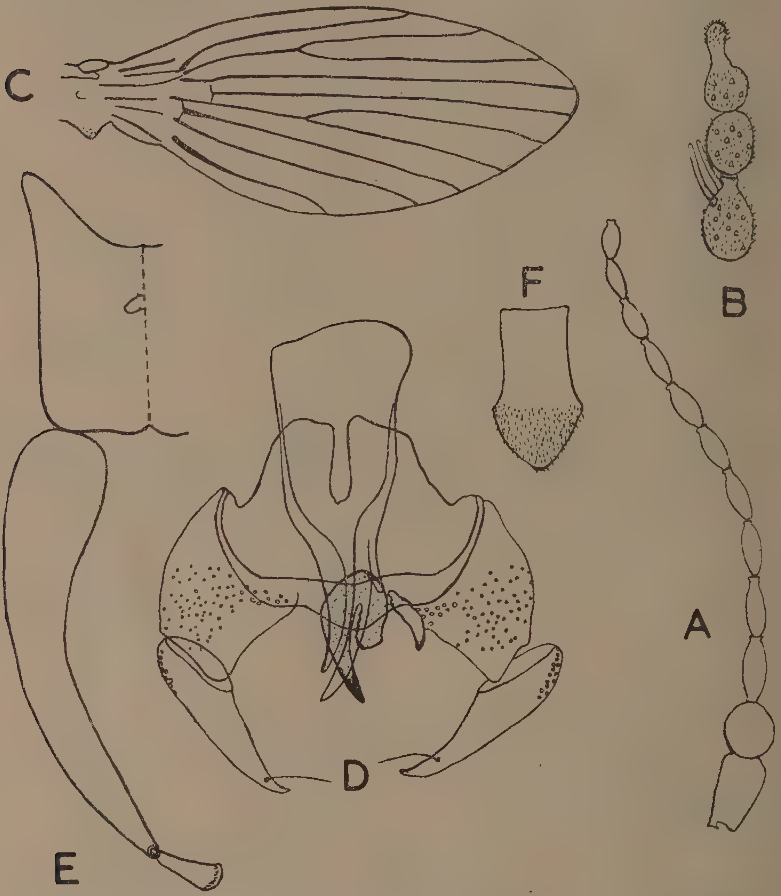

Fig. 1.—*Pericoma clarkei* sp. n. A. Basal twelve segments of antenna. B. Tip of antenna. C. Venation. D. Hypopygium. E. Cercopod. F. Anal flap.

Descriptions of New Species.

Pericoma clarkei sp. n.

A large whitish-brown species with two prominent white spots in the middle of each wing.

Male.—Decumbent whitish tuft on clypeus, erect tuft on face. Eye bridges four facets wide, separated by width of 4 facets; antennae (fig. 1A) 16 segmented, 0·75 of wing width, verticils open; scape 1·5 times as long as broad, basal flagellar segment barrel-shaped, three times as long as wide, last three (fig. 1B) almost spherical, terminal one with a clubbed apiculus as long as the basal bulb; ascoids simple, paired, on segments 4–14. Palpal formula 1 : 2·1 : 2·2 : 3·3.

Thorax with a long whitish vestiture, no allurement organ present. Wing (fig. 1C) 2·7 mm. long, apex between the tips of R_4 and R_5, Sc almost joining to R_1, radial fork slightly before medial, both in middle of wing; origin of R_{2+3} considerably before apex of first basal cell which is much longer than the second; erect hairs absent on R_5 and M_4, extending along remaining veins approximately to level of tip of R_2; wing vestiture brown (probably darker in fresh specimens) with a prominent patch of erect white hairs at the wing base, another extending along R_1, R_2 and R_3 from level of radial fork to just before tip of R_1, and a third extending along M_1, M_2 and M_3 from just past medial fork to just before level of tip of M_4; wing fringe brown apart from an apical white patch extending from tip of R_3 to tip of M_1; wing membrane infuscated except in two areas underlying the medial white patches; hairs on underside of wing whitish in these areas. Legs brown with whitish apical rings on tibiae, metatarsi, and first tarsal joints.

Abdomen with long whitish vestiture. Hypopygium (fig. 1D) with ninth sternite deeper medially, coxite broad, style broad, sub-equal to coxite, very slightly curved, tapering evenly to tip, with a single preapical seta; aedeagus with ejaculatory apodeme broad, its edges inrolled and extended parallel to each other posteriorly to form median portion of aedeagus, a heavily sclerotised U-shaped lump of cuticle overlying these with one arm pointed and longer than the other which ends irregularly; an irregular strip of sclerotised cuticle on the base of the coxite articulating with this; cercopods (fig. 1E) three times as long as ninth tergite with a single broad retinaculum one-sixth of length of cercopod; anal flap shaped as in fig. 1F.

Type and 1 ♂ *paratype*, Hump Mt. (52 miles, directly W.N.W. of Invercargill, 2–3,000 ft.), 3.i.1922 (*C. E. Clarke*). 1 ♂ *paratype*, Harris Saddle near Nelson 4.i.1945 (*E. S. Gourlay*).

This very distinct species, related to the *triuncinata-drepanata* group of species, is named after the late Mr. C. E. Clarke who collected the type and one paratype. These specimens are in the Auckland Museum. The other specimen is in the Tonnoir collection at the Cawthron Institute, Nelson.

Pericoma solitaria sp. n.

Closely related to *Pericoma drepanata* Sat., but with the radial fork more loosely connected and the male genitalia quite distinct.

Male.—Head vestiture brown, eye bridges separated by width of two facets. Antennae 16 segmented, four-fifths of wing width; scape (fig. 2A) 1·2 times as long as wide, basal flagellar segments barrel-shaped, 1·3 times as long as wide, becoming smaller and shorter, last three subspherical, terminal apiculus (fig. 2B) equal to bulb; ascoids two to four branched. Palpi not investigated.

Thorax with brown hairy covering, no allurement organ present. Wing (fig. 2C) 2·1 mm. long, apex just above tip of R_5, both forks at same level, well before tip of Cu; R_3 not joined to R_2 proximally, origin of radial fork well after apex of first basal cell which is considerably longer than the second; wing vestiture light brown, with darker tufts of erect hairs at apex of first basal cell, over forks and at tip of Cu; reclined hairs forming a darker fascia on all veins at level of tip of M_4; whitish erect hairs on R_1, R_4 and M_3; fringe unicolourous. Legs mostly missing on type, but first tibia with a whitish apical ring.

Hypopygium (fig. 2D) with coxites short and cylindrical, styles shorter than coxites, basally swollen and very abruptly narrowed to a short almost straight blade; a large preapical seta; aedeagus consisting of a median element bent near the tip and a shorter straight element beside it; cercopod much curved, evenly tapered, 2·4 times as long as ninth tergite; retinaculum single, one sixth length of cercopod; anal flap-shaped as in Fig. 2F.

Female.—Unknown.

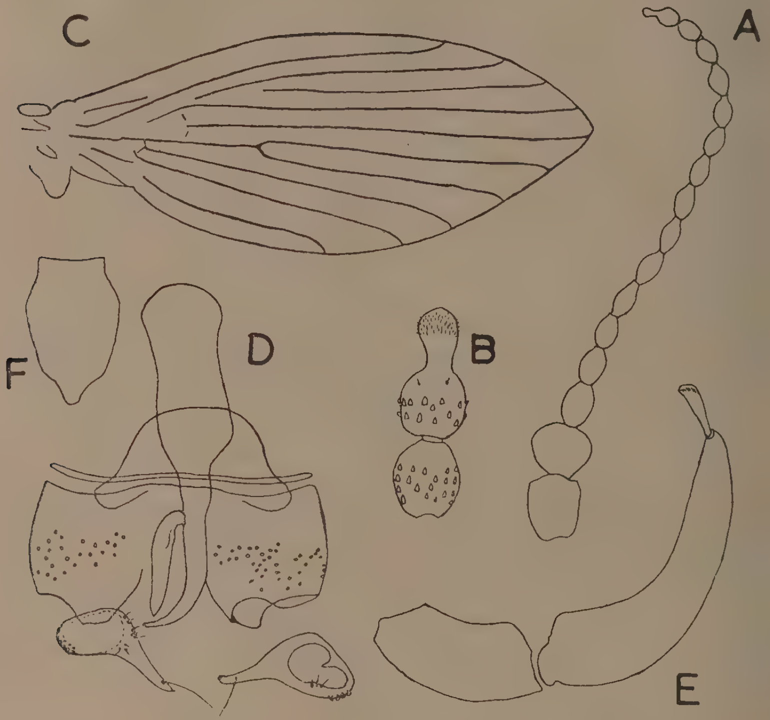

FIG. 2.—*Pericoma solitaria* sp. n. A. Antenna. B. Tip of antenna. C. Venation. D. Hypopygium. E. Cercopod. F. Anal flap.

Type: Te Aroha, 1.iii.1923 (*A. L. Tonnoir*).

Tonnoir partially described this species in his MSS notes and provided the name used above. In my 1950 paper I distinguished between the three similar species *P. drepanata*, *P. claviata* and *P. triuncinata*, all of which have a similarly patterned wing, and *P. maura* which is uniformly brown. *P. solitaria* is even less patterned than the other three patterned species, and I now feel that *P. maura* should be associated with these four in a single group of species. Under the label *P. pseudomaura* is a uniformly brown specimen, originally collected and described in note form by Tonnoir, which is identical in genitalia and venation with *P. drepanata* and is to my mind merely a patternless form of it. It is thus apparent that the distinctness of the patterning may vary much within a species—a conclusion amply borne out in such well known species as *Psychoda alternata* Say—and that species separated off on grounds of colour patterning alone are likely to be abandoned with the collection of further material.

Pericoma furcata Satchell.

Satchell, G. H., 1950, *Trans. R. ent. Soc. Lond.* 101 : 163.

In using this name I created a homonym, since Kincaid described a species under this name in 1899. I am indebted to Dr. Allan Stone for drawing my attention to this. I would like to substitute the name *P. diffusa* for *P. furcata* Satchell, 1950. This name was originally suggested by Tonnoir for this species in his MSS notes, and was abandoned by me in the mistaken impression that it was already in use.

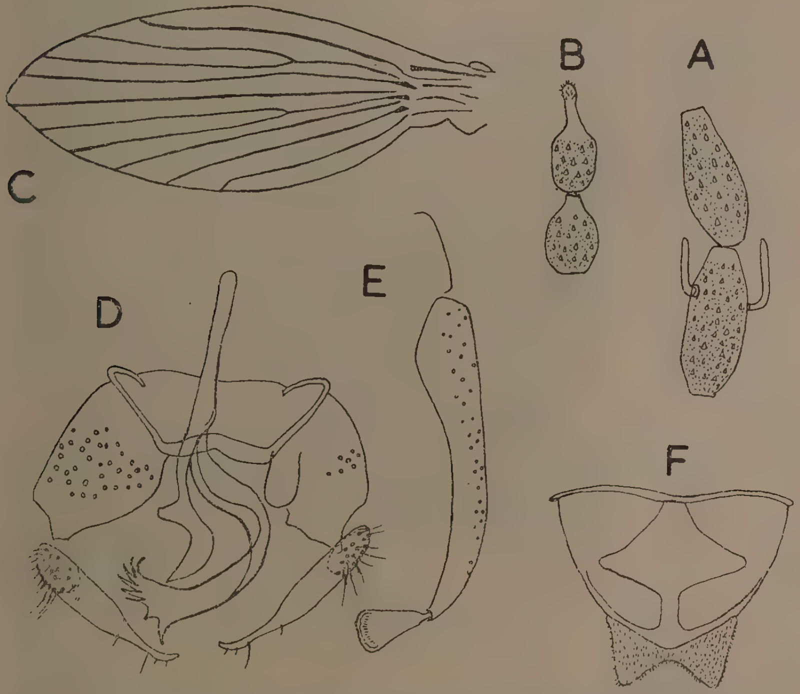

Fig. 3.—*Pericoma barbata* sp. n. A. Basal flagellar segments of, B. tip of antenna. C. Venation. D. Hypopygium. E. Cercopod. F. Subgenital plate.

Pericoma barbata sp. n.

A golden-yellow species with characteristic male genitalia belonging to the *lobisterna-spiralifera* group of species.

Male.—Decumbent whitish-yellow tuft of squamose hairs on clypeus, erect tuft on face, decumbent fringe on vertex. Eye bridges 3 facets wide, separated by width of 2 facets. Antennae 16 segmented, almost (10·5 : 11) as long as wing width ; basal flagellar segments (fig. 3A) 2·6 times as long as wide, last three segments (fig. 3B) more nearly spherical, 1·8 times as long as broad, with a clubbed apiculus almost as long as the basal bulb ; ascoids paired simple rods (fig. 3A).

Thorax with long yellow hairy vestiture ; anepisternite with yellow hairy tuft, but with no allurement organ. Wing (fig. 3C) with Sc long and straight, not joined to R_1, wing apex a little above tip of R_5, radial fork very slightly before medial, both before middle of wing ; origin of R_{2+3} at apex of first basal cell which is equal to the second ; erect hairs absent on R_5, and M_4, extending to just short of the tips on R_1, R_2, M_2 and M_3, and to the level of the tip of M_3 on R_3, R_4 and M_1 ; wing vestiture and legs uniformly yellow.

Abdomen with tufted hairy vestiture. Hypopygium (fig. 3D) with ninth sternite squarish at the corners, transverse, slightly indented medially ; coxites cylindrical with a narrow but distinct infra-basal process ; style longer than coxite, parallel sided in basal two-thirds, narrow and curved in apical third, with a prominent seta just before the curved portion ; aedeagus consisting of one curved pointed element, and a second curved element of larger size terminating in a broad blade frayed out into points ; cercopods (fig. 3E) very long and slender with a single broad spatulate retinaculum.

Female.—Very similar to male with subgenital plate as in fig. 3F, the lobes meeting across the middle. Spermathecae not well displayed in material available, ovipositor twice as long as subgenital plate.

Type, *allotype*, and 4 ♀ *paratypes*, Leith Valley, Dunedin, 11–29.xi.1949.

This species was collected on the shady under surfaces of some rocks forming part of a waterfall in the Leith stream ; some *Pericoma* larvae that were found on the wet stones splashed by the waterfall in all probability belong to this species, though I was unable to breed them out.

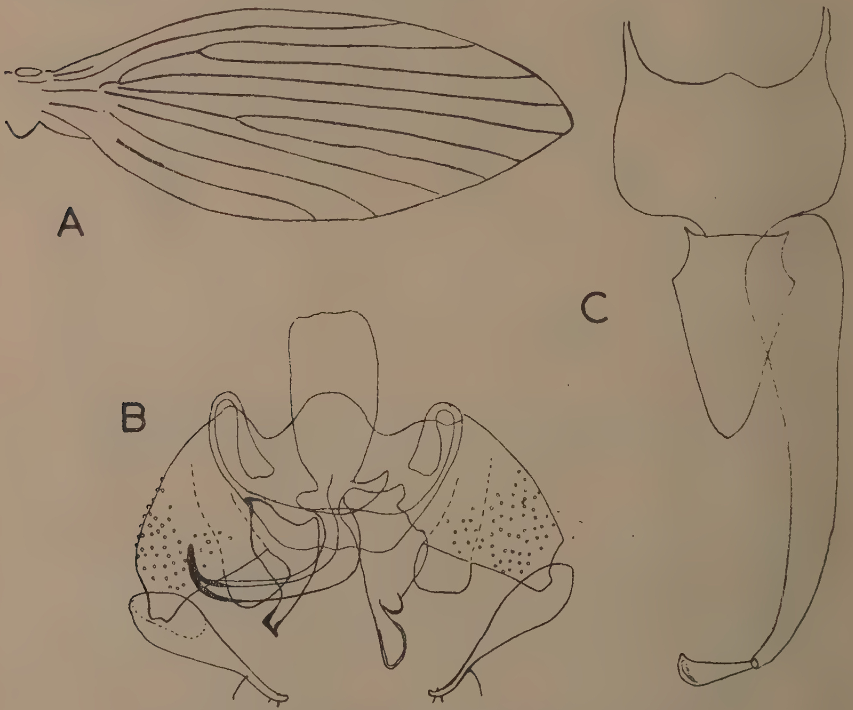

FIG. 4.—*Pericoma bilobata* sp. n. A. Venation. B. Hypopygium. C. Cercopod and anal flap.

The name of this species was originally suggested by Tonnoir in his MSS notes, and a pencil sketch of the male genitalia was included but no specimens of it are now to be found in Tonnoir's collection, and he left no further description of it. It is very closely related to *P. bifalcata* Satchell and *P. spiralifera* Satchell, from which it can be differentiated only by the male genitalia. The females cannot be distinguished with any certainty.

Pericoma bilobata sp. n.

Uniformly golden-yellow species separated from *Pericoma spiralifera* Satchell only by small differences in the style and aedeagus.

Male.—Decumbent tuft of white squamose hairs on clypeus, erect tuft on face and epicranium. Eye bridges separated by width of 2 facets. Antennae missing.

Thorax with a slightly more whitish vestiture than in *P. spiralifera*, wing (fig. 4A) 2·5 mm. long with apex just above R_5, radial fork before medial, which lies above the middle of Cu; origin of R_{2+3} at apex of first basal cell which is equal in length to the second; wing vestiture and legs uniformly golden.

Hypopygium (fig. 4B) with ninth sternite as in *P. spiralifera*; infrabasal process of coxite projecting beyond its inner margin; style rather more curved at the tip; aedeagus consisting of (*a*) a central element with two right angular bends, ending in a simple pointed tip; (*b*) a lateral element to one side with a squarely ending process projecting posteriorly and a less prominent lateral tooth near the base and (*c*) a broad lateral element on the other side, of irregular shape, narrowing posteriorly to a rounded spatulate lobe; cercopod (fig. 4C) long, gently tapering, three and a half times as long as ninth tergite with a single apical retinaculum 0·14 of length of cercopod; anal flap as in fig. 4C, exactly as in *P. spiralifera.*

Type (only specimen): Waiho, 21.i.1922 (*A. L. Tonnoir*).

Tonnoir originally suggested the name for this species. It is closely related to *P. spiralifera* and the two species *P. serratipenis* Sat. and *P. diffusa* Sat. have very similar genitalia, though in these the wing is distally infuscated.

Tonnoir has included two females along with the single type male, but in his notes on this species he does not say on what evidence they are associated and writes the word " supposed " at the side of the notes on them. I have not therefore described them.

Psychoda pulchrima sp. n.

A large grey species with long antennae and two white spaces in the posterior wing fringe.

Male.—Decumbent grey tuft on clypeus, erect grey hairs on face, between eyes and on epicranium. Eye bridges unusually wide, 5–6 facets wide, separated by width of one facet. Antennae 16 segmented, 1·8 times wing width, verticils long, almost closed; scape (fig. 5A) 1·5 times as long as wide, basal flagellar segment with neck 1·7 times as long as bulb, twice as long in subsequent segments; segment 13 (fig. 5B) with short neck, segments 14–16 diminutive, well separated; ascoids with very long annulated arms (fig. 5B) on segments 3–13, paired sensory cones inserted near bases of ascoids. Palpal formula 1 : 1·6 : 1·6 : 1·8.

Thorax with predominantly greyish hairy vestiture. Wing (fig. 5C) 2 mm. long, radial fork in middle of wing, after medial, before tip of Cu; origin of R_{2+3} a very little after apex of first basal cell which is very little longer than second; erect hairs absent from R_5, M_2 and M_4, present to tips of remainder; wing fringe greyish apart from two creamy-white spaces, one starting above tip of M_3 and extending to half way between tips of M_3 and M_4, and the other starting at tip of Cu and extending towards wing base for a distance slightly greater than that of the first one.

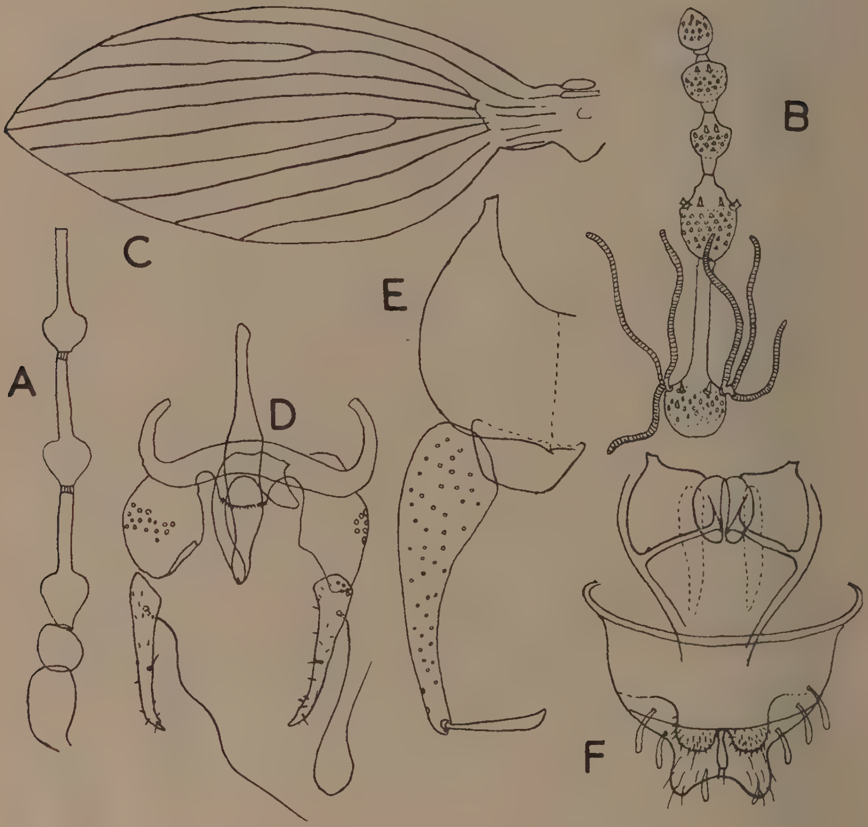

Fig. 5.—*Psychoda pulchrima* sp. n. a. Base of, b. tip of antenna. c. Venation. d. Hypopygium. e. Cercopod. f. Subgenital plate and spermathecae.

Abdomen with hairy vestiture. Hypopygium (fig. 5d) with ninth sternite a simple sclerotised band ; coxite a little shorter than style which is almost straight, slightly curved at tip, and has a very long seta inserted near the base, and numerous small setae scattered along the length ; basal lateral tuft consisting of very few hairs ; aedeagus composed of a median piece with a rather spatulate tip and a curved lateral piece placed close up against it ; median ventral pilose lobe as in fig. 5d ; cercopods (fig. 5e) twice as long as ninth tergite when measured in mid ventral line, bearing a single retinaculum one third of length of cercopod.

Female.—Similar to male but eyes slightly more separated, ascoids a little shorter. Subgenital plate shaped as in fig. 5f, covered with a vestiture of squamose hairs ; with a club-shaped genital digit ending in two setulae ; paired capsules lying below subgenital plate, with a hairy lining ; spermathecae as in fig. 5f with rather elongate capsules ; inner capsules devoid of reticulation ; ovipositor 1·5 times as long as subgenital plate.

Type, *allotype* and 7 ♂, 4 ♀ *paratypes*, 4 ♂, 8 ♀ other specimens, Leith Valley, Dunedin, 11–24.xi.1949. ♀ South Warrington, Otago, 20.ii.1950.

This very characteristic species was swept from herbage bordering a small waterfall in the Leith Stream, and in a similar habitat near Warrington. I have recently seen specimens of this species from Campbell Island, and it is probably widely distributed in the cooler parts of New Zealand.

Psychoda formosa sp. n.

A rather small yellowish-brown species with lanceolate wings.

Male.—Decumbent yellowish tuft on clypeus; erect bushy tuft on face. Eye bridges 3–4 facets wide separated by width of 2 facets. Antennae 16-segmented, 1·5 times wing width, verticils rather yellow and open; scape (fig. 6A) 1·8 times as long as broad, neck shorter than bulb in basal flagellar segment, longer than bulb in succeeding segments until it is 1·5 times as long in segment 10; segment 13 with very little neck, segments 14–16 (fig. 6B) diminutive, subspherical, well separated; ascoids Y-shaped, with very long anterior arms on segments 3–13. Palpi scaly, yellowish, formula not investigated.

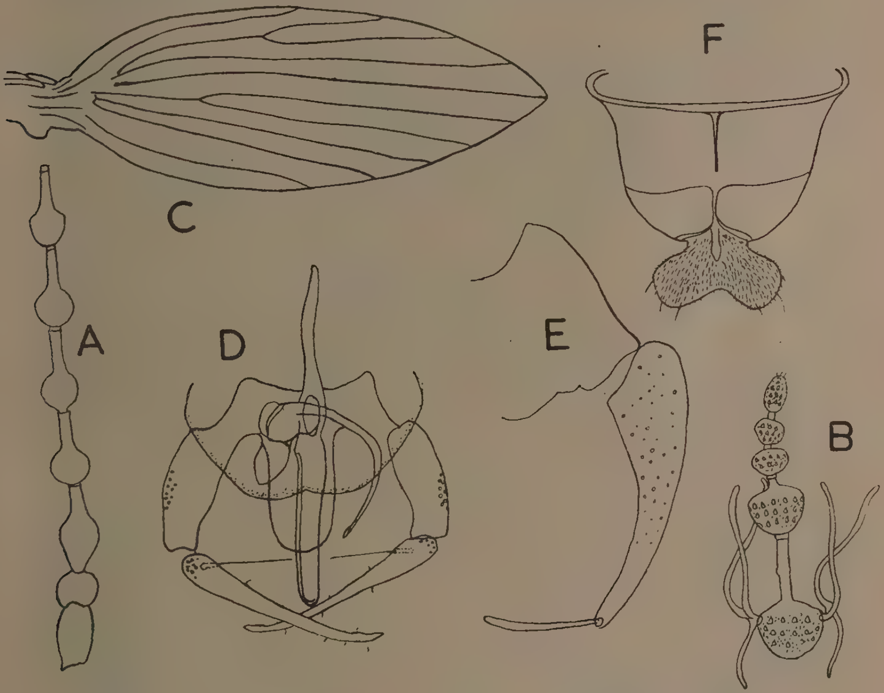

Fig. 6.—*Psychoda formosa* sp. n. A. Base of, B. tip of antenna. C. Venation. D. Hypopygium. E. Cercopod. F. Subgenital plate.

Thorax with yellowish hairy vestiture. Wing (fig. 6C) lanceolate, 1·7 mm. long, interfork distance one-seventh of wing length, radial fork after medial, both before tip of Cu; origin of R_{2+3} very slightly after apex of first basal cell which is considerably longer than the second; erect hairs to tips of usual veins; legs and wings unicolorous.

Abdomen with yellowish vestiture. Hypopygium (fig. 6D) with ninth sternite semicircular and indented in mid line; coxites narrow and shorter than styles which are very long, almost straight and bear a long basal seta and a few short scattered setae more distally; lateral tuft of deciduous hairs on base of style and side of coxite much reduced; aedeagus consisting of (*a*) a long straight median element with a rounded spatulate end; (*b*) a curved element with a pointed tip lying across it basally but with the tip well to the side of the main piece; (*c*) a short, flat, heart-shaped piece on the other side; a long parallel sided lobe with a rounded end present ventrally under the aedeagus. Cercopods (fig. 6E) almost twice as long as ninth tergite, evenly tapered from base to tip, bearing a single retinaculum 0·4 times as long as cercopod.

Female.—Similar to male. Subgenital plate with lobes shaped as in fig. 6F, separated by a shallow medial emargination. Spermathecae damaged in allotype and only female, ovipositor twice as long as subgenital plate.

Type, allotype and 2 ♂ *paratypes*, Leith Valley, 11–19.xi.1949. 1 ♂ *paratype*, Waiho, 30.i.1922 (*A. L. Tonnoir*). 1 ♂ *paratype*, Aniseed Valley, 8.ix.1922 (*A. Philpott*). 1 ♂ *paratype* Lake Brunner, 3.ii.1922, (*A. L. Tonnoir*).

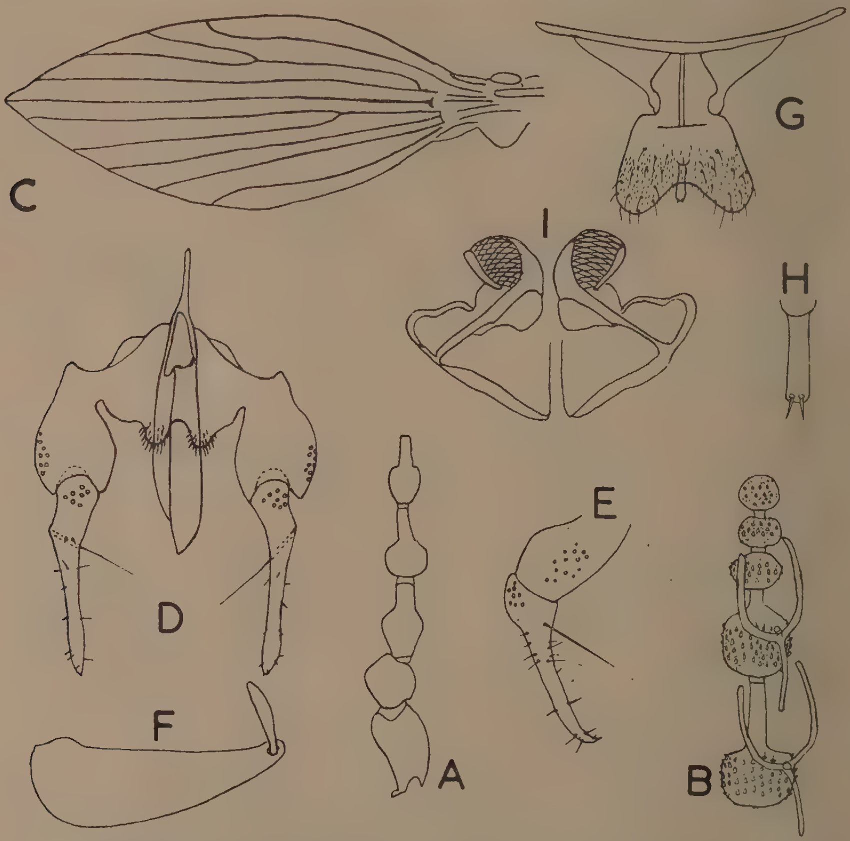

FIG. 7.—*Psychoda simplex* sp. n. A. Base of, B. tip of antenna. C. Venation. D. Hypopygium. E. Coxite and style in lateral view. F. Cercopod. G. Subgenital plate. H. Genital digit. I. Spermathecae.

The four specimens I collected were swept from grass bordering a small waterfall in the Leith Stream.

Psychoda simplex sp. n.

A small greyish-ochraceous species with the aedeagus consisting of a single element.

Decumbent tuft on clypeus, erect tuft on face; eye bridges separated by width of 1 facet. Antennae 16 segmented, 1·6 times as long as wing width, with greyish closed verticils; scape (fig. 7A) 1·6 times as long as broad, basal flagellar segment with neck equal to bulb; neck 1·6 times as long as bulb in segment 10; segment 13 with a distinct neck, 14–16 diminutive, subspherical, well separated (fig. 7B); ascoids Y-shaped; arms a little unequal. Palpal formula 1 : 1·1 : 1·3 : 1·7.

Thorax with hairy covering. Wing (fig. 7C) 1·8 mm. long, radial fork after medial, both before tip of Cu; origin of R_{2+3} well after apex of first basal cell which is a little longer than second. Erect hairs to tips of usual veins. Legs and wings uniformly greyish. Hypopygium (fig. 7D) with styles longer than coxites, little curved, slightly hooked at tip when seen in profile (fig. 7E) with one large seta near the base, and a few short sensory seta occurring along the length; lateral tuft at base of style and of coxite composed of rather few squamose hairs; aedeagus (fig. 7D) formed of a single straight element, slightly spatulate at the tip in certain views; paired hairy lobes ventrally at sides of aedeagus. Cercopods (fig. 7F) 1·4 times as long as ninth tergite, tapering evenly to tip, with a single retinaculum one-third as long as cercopod.

Female.—Similar to male. Subgenital plate (fig. 7G) with sides approaching each other anteriorly, medial emargination narrow; genital digit long (fig. 7H) cylindrical, terminating in two small setulae; spermathecae (fig. 7I) with reticulate inner capsules. Ovipositor 2·5 times as long as subgenital plate.

Type, *allotype* and 9 ♂, 10 ♀ *paratypes*, 10 ♀ other specimens, Bullock track, North Dunedin, 2.ix–1.xi.1949.

This species is common in the early part of the year on a wet rock surface where a small stream trickles over a shaded vertical rock wall along the Bullock track. This track is well in the town of Dunedin and the species has so far been taken only in this single locality. *Psychoda inaequalis* Sat. is also abundant in this habitat.

Psychoda tridens sp. n.

A medium sized greyish species related to *P. cinerea* Banks, with three elements in the aedeagus.

Male.—Decumbent tuft of squamose hairs on clypeus, erect tuft on face. Eye bridges separated by width of 1½ facets. Antennae 16 segmented, 1·6 times wing width, scape and pedicil with scaly covering, verticils whitish-grey, closed; scape (fig. 8A) 1·5 times as long as wide, basal flagellar segment with neck longer (1·2) than bulb, increasing in length in subsequent segments until it is 1·8 times as long in segment 10 (fig. 8C); segment 13 with a short neck, 14, 15 and 16 diminutive, subspherical, well separated (fig. 8B); ascoids three-branched, anterior arms long, reaching to tip of neck, distinctly annulated. Palpi with a scaly covering, palpal formula 1 : 1·2 : 1·2 : 1·5.

Thorax with a covering of greyish-ochraceous hairs with smaller whitish scales interspersed, particularly in the midline and above the anterior spiracle. Wing (fig. 8D) 2·4 mm. long, radial fork after medial, both before tip of Cu; origin of R_{2+3} very considerably past apex of first basal cell. Interfork distance one eighth of wing length. Erect hairs present to tip of all veins except R_5, M_2 and M_4. Vestiture uniformly greyish, legs greyish.

Abdomen with long hairy vestiture; genitalia with a sparse scaly covering. Hypopygium (fig. 8E) with ninth sternite rounded laterally; coxite equal to, sometimes longer than, style; style bent ventrally, hooked at the tip, with one long seta near the base and a number of smaller ones scattered over the surface; three of these presenting a characteristic configuration on the outer edge of the style when seen in profile; aedeagus consisting of (*a*) a large median rather spatulate element; (*b*) a long pointed element laid across it, and (*c*) a short pointed element which is a process of (*a*); a single median bristly lobe present ventrally. Cercopod (fig. 8F) 1·2 times as long as ninth tergite; tapering evenly from a swollen base to a point four-fifths of the way along where there is a more abrupt narrowing; retinaculum single, 0·35 as long as cercopod.

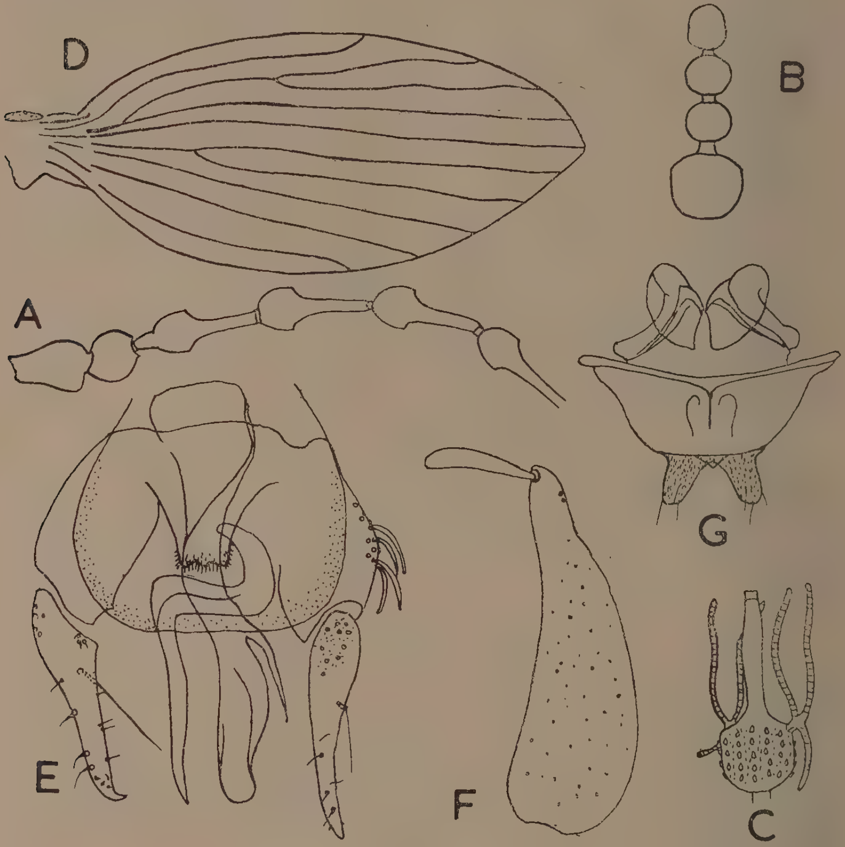

FIG. 8.—*Psychoda tridens* sp. n. A. Base of, B. tip of antenna. C. Medial antennal segment with ascoids. D. Venation. E. Hypopygium. F. Cercopod. G. Subgenital plate and spermathecae.

Female.—Similar to male but antennal segments with shorter necks. Subgenital plate (fig. 8G) with pilose lobes almost separated by the deep median indentation; genital digit almost absent, represented only by a conical protuberance. Spermathecae as in fig. 8G, with simple non-reticulate capsules. Ovipositor 2·4 times as long as subgenital plate.

Type, *allotype* and 5 ♂, 2 ♀ *paratypes*, 7 ♂, 4 ♀ other specimens, Leith Valley, Dunedin, dates from 9.ix.1949–19.xi.1949. 4 ♂, 2 ♀ *paratypes*, 3 ♂, 8 ♀ other specimens, Ross Creek, Dunedin, 14.ix–4.xi.1949.

This species is quite common amongst the grass bordering the Ross and Leith streams in the early spring. It was the first species to appear in the spring of 1949.

SUMMARY.

The following eight new species of New Zealand Psychodidae are described : *Pericoma clarkei*, *P. solitaria*, *P. barbata*, *P. bilobata*, *Psychoda pulchrima*, *P. formosa*, *P. simplex* and *P. tridens*.

The new name *Pericoma diffusa*, is substituted for *Pericoma furcata* Satchell 1950, which is a primary homonym with *Pericoma furcata* Kincaid, 1899.

A key is provided to the forty-three described species of New Zealand Psychodidae.

ACKNOWLEDGMENTS.

I should like to thank Mr. E. G. Turbott for lending me specimens from the Auckland collections, Mr. R. A. Harrison, for the loan of specimens, and Mr. E. S. Gourlay, for assistance in identifying the type locality of *Pericoma clarkei* sp. n.

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A REVISION OF THE GENUS *APHNAEUS* HÜBNER (RHOPALOCERA : LYCAENIDAE).

By H. Stempffer, F.R.E.S.

Manuscript received 28th May, 1953.

(Read 5th May, 1954.)

With 2 Plates and 18 Text-figures.

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1. History of the Genus.

The genus *Aphnaeus* was erected by Hübner in 1823 (*Verz. bekannt. Schmett.* **6** : 81) for two species: *Papilio vulcanus* Fabricius, 1775, and *Papilio orcas* Drury, 1782. In fact these two species are not congeneric : *vulcanus* Fabricius, an Indo-Malayan species, is what we now call a *Spindasis*. Scudder in 1875 (*Proc. Amer. Acad. Arts Sci.* **10** : 116) selected *orcas* as the type species of the genus *Aphnaeus*.

Aurivillius in *Rhopalocera Aethiopica* (1898) included in *Aphnaeus* the following species :

A. orcas (Drury, 1782), *A. propinquus* Holland (1893), *A. argyrocyclus* Holland (1890), *A. hutchinsoni* Trimen (1887) with, as a synonym, *zanzibarensis* Smith (1889), *A. erikssoni* Trimen (1891), *A. asterius* Plötz (1880) with, as synonyms, *chalybeatus* E. Sharpe (1890) and *ilogo* Holland (1893), and *A. argenteola* Holland (1890).

In Seitz' *Macrolepidoptera of the World*, **13**, Aurivillius (1923) added to the preceding species *A. brahami* Lathy (1903), *A. drucei* Neave (1904), *A. rex* Aurivillius (1909), *A. questiauxi* Aurivillius (1903) and *A. marshalli* Neave (1910). He omitted to mention *A. affinis* Riley (1921) and treated *argenteola* Holland as an aberration of *asterius* Plötz.

Later on *A. neavei* Bethune-Baker (1926), *A. jefferyi* Hawker-Smith (1928), *A. coronae* Talbot (1935) and *A. bruneeli* Berger (1951) were described.

2. Method of Revision.

I have dissected the male genitalia of all the known species of *Aphnaeus*. The genus is so homogenous that they all belong to the same type, the specific characters shown by the armature usually being not easily distinguished, even when the species are widely separated in the colour and patterns of the wings.

I have therefore given a detailed description as well as a figure of the male armature of the type species, *Aphnaeus orcas*, only, and figures only of the other species. Fortunately, they differ enough in their external facies to make possible fairly easy identification.

3. ACKNOWLEDGMENTS.

I should not have undertaken this revision if I had not been encouraged by Mr. N. D. Riley, who allowed me to work on the British Museum material and gave me valuable advice on the intricate questions of the *asterius* and *erikssoni* groups. Through the kindness of Dr. L. Berger I was also able to examine the collections of the Musée du Congo Belge, Tervuren, and Mr. T. H. E. Jackson of Kitale and Dr. van Someren of Ngamy lent me numerous specimens from Kenya, including several new species and forms. I wish to express my best thanks to all those who have helped me in my task.

4. SYSTEMATIC REVISION.

Aphnaeus Hübner (1823).

Type species: *Papilio orcas* (Drury, 1782).

Eyes with dense short hair. Palpi moderately long, parallel, the second joint long, slightly ascending, densely covered with scales, the third joint very short, horizontal, slender, with a blunt tip. Length of antenna three-fifths of that of costa of fore wing, club progressively swollen, not sharply differentiated.

Fore legs of male: Tibia as long as femur, tarsi not articulated.

Wing shape.—Fore wing: Costa slightly arched at the base, then straight, apex very acute, external border slightly convex from the apex to vein 4, then straight or even slightly concave. *Hind wing:* Strongly produced towards the anal angle, marginal border slightly scalloped, a fine tail at the extremity of vein 2, another also fine but much longer one at the extremity of 1*b*, a lobe at the anal angle.

Wing venation.—Fore wing with 12 veins; 3 from a little before the lower angle of cell, 4 from this angle, 5 nearer to 6 than to 4, 6 from the upper angle of cell, 7 also from this angle and reaching the external border a little below the apex, 8 and 9 stalked upon 7, 10 and 11 free from the upper border of the cell. *Hind wing:* 3 and 4 from the lower angle of the cell, 5 equidistant from 4 and from 6, 6 from the upper angle of the cell, 7 from before this angle.

Male genital armature: see under *orcas*.

Aphnaeus orcas Drury (Text figs. 1 and 2).

Papilio orcas Drury, 1782, *Illust. Exot. Ins.* 3 : 46, pl. 34, fig. 2, 3.

The external facies of this species is so well known that a new description is not necessary.

Male genital armature: slides nos. 1482, 1492, Katera, Uganda. Uncus reduced to a narrow strip edging the tegumen. Subunci long and curved at an acute angle, with a blunt tip. Tegumen subrectangular (in its normal position hood-shaped). Cingula of moderate width with a short rounded saccus. Fultura inferior formed of two flattened arms, its base fused with the base of the valvae, near the cingula, but at about the middle of their total length. Valvae longish, the two processes (superior and inferior) entirely separated in the distal half and both with a rounded apex, the superior process more slender and a little longer; a small, weakly chitinised band uniting the two superior processes, crossing above the external part of the penis; this last is thus encircled by the body of the valvae themselves and this median band. Penis large, the upper edge showing a protuberance a little beyond the wall of the genital opening ; the external part evenly diminishing in diameter up to the blunt end; in its basal part the penis bears a tuft of long and strong spines, in its median part and at the tip, two groups of cornuti. Uncus and distal part of valvae hairy.

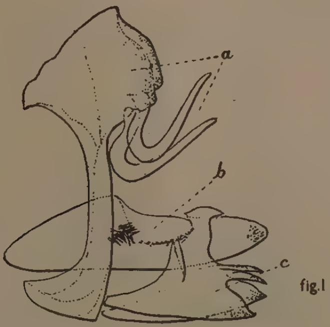

FIG. 1.—Male genitalia of *Aphnaeus orcas* Drury in lateral view. *a*, tegumen and subunci, *b*, penis, *c*, valvae.

This sheathing of the penis by the valvae is not peculiar to the genus *Aphnaeus* ; similar cases are found in the whole subfamily Aphnaeinae which contains the following genera : *Aphnaeus*, *Cigaritis*, *Apharitis*, *Spindasis*, *Chloroselas*, *Zeritis*, *Desmolycaena*, *Axiocerses*, *Phasis* and *Erikssonia*. The median connecting band of valvae is translucent, fragile and during dissection it is rather difficult to extract the penis without breaking it. When torn, it can be easily overlooked, being mistaken for an unimportant membrane.

Habitat : Western Africa from Sierra Leone to Gaboon, French and Belgian Congo, Uganda.

Aphnaeus orcas hollandi Butler.

A. hollandi Butler, 1902, *Proc. zool. Soc. Lond.* **1902** : 49, pl. i, fig. 7.
A. rattrayi E. Sharpe, 1904, *Entomologist* **37** : 203.

Differs from the typical form by the following characters :

Male: *wings, upperside :* Blackish-brown spots of fore wing more developed ; in extreme specimens, those situated between 6 and 4 fuse with the apical spot which also is larger. *Underside :* Dull yellowish-brown ; all the silvered spots and stripes encircled with a ferruginous-red edge, in fore and hind wing anteterminal stripe carmine or ferruginous-red, encircled small silvered spots often reduced in number, anal lobe orange or yellowish instead of carmine red.

Male genitalia : Identical to those of *orcas orcas*.

Female : Similar to the typical form.

Described by Butler from the " Congo Forest." Aurivillius in Seitz, **13** : 408, considers *hollandi* as the southern and eastern race of *orcas* (Congo, Toro), but ascribes to it a " darker underside," a statement which is exactly the opposite of the truth, since Drury described the ground colour of *orcas* as " fine red

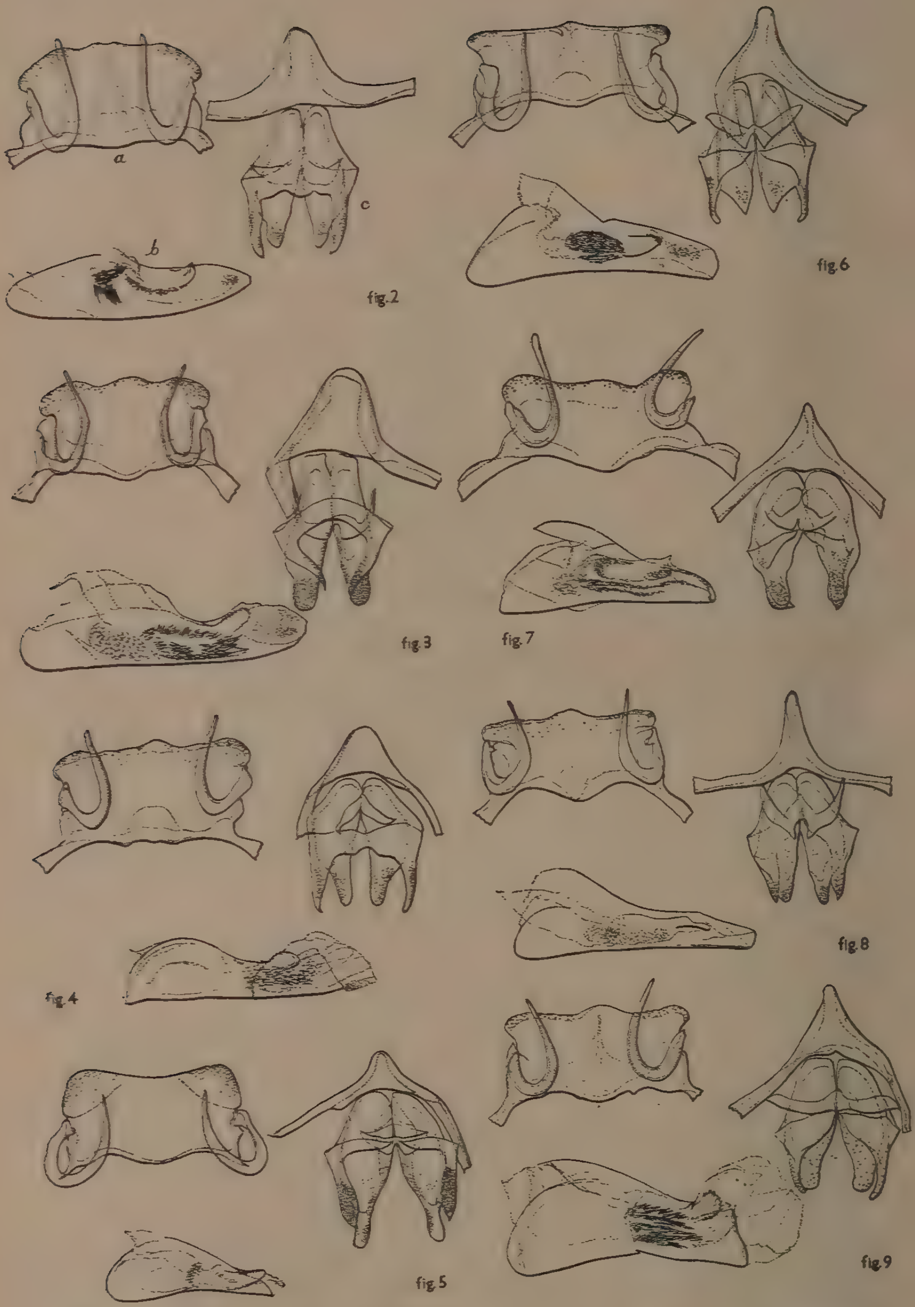
a
b
c
fig.2
fig.6
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fig.9

FIGS. 2–9.—Male genitalia in *Aphnaeus*. (2) *orcas* Drury ; (3) *argyrocyclus* Holland ; (4) *nyanzae* sp. n. ; (5) *chalybeatus* Sharpe ; (6) *questiauxi* Aurivillius ; (7) *brahami* Lathy ; (8) *jefferyi* Hawker Smith ; (9) *erikssoni* Trimen. *a*, tegumen and subunci, *b*, penis, *c*, valvae.

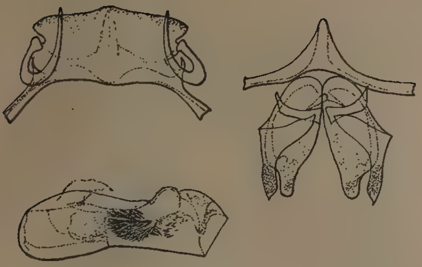

fig.10

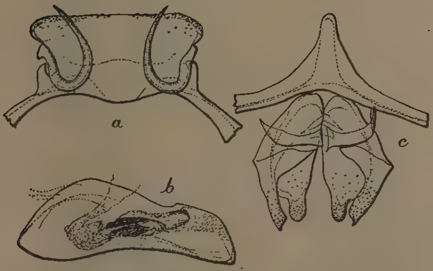

fig.11

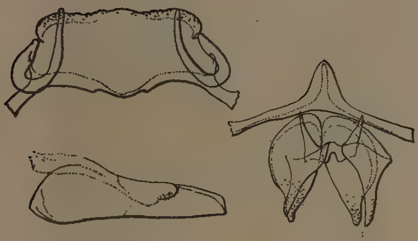

fig.12

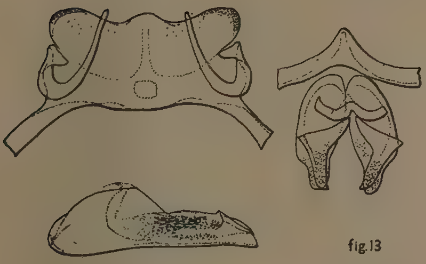

fig.13

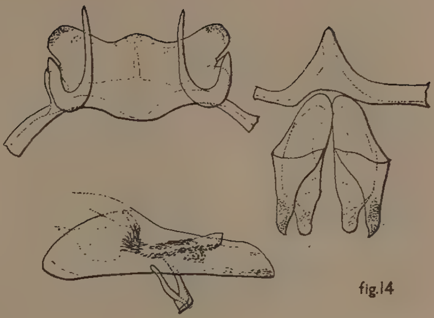

fig.14

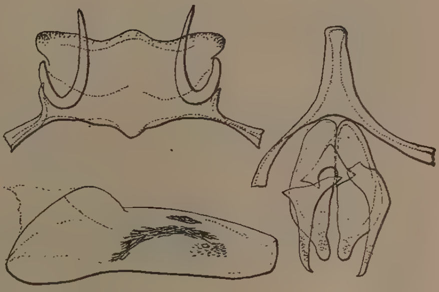

fig.15

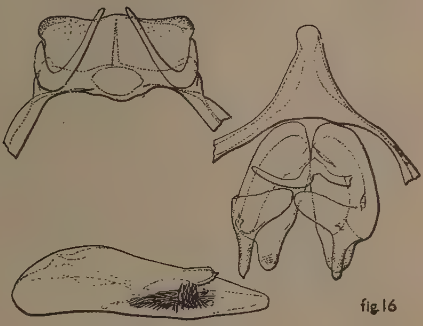

fig.16

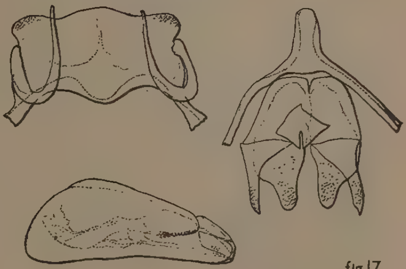

fig.17

FIGS. 10–17.—Male genitalia in *Aphnaeus*. (10) *affinis* Riley; (11) *marshalli* Neave; (12) *neavei* Bethune-Baker; (13) *coronae* Talbot; (14) *jacksoni* sp. n.; (15) *adamsi* sp. n.; (16) *flavescens* sp. n.; (17) *hutchinsoni* Trimen. *a*, tegumen and subunci, *b*, penis, *c*, valvae.

brown, almost as deep as chocolate ", and Butler that of *hollandi* as " palish earthy brown " in fore wing, " yellowish stone colour suffused with grey " in hind wing.

I have examined specimens from Katera (Uganda), which agree well with Butler's description of *hollandi*. In Kenya (Nandi) and Katanga, the species appears to be very variable and most of the specimens show transitional characters : blackish-brown spots of fore wing upperside more or less developed, ground colour of underside running from reddish-brown to light yellowish-brown. However, the lines of carmine red or ferruginous red scales encircling the silvered spots always remain visible, also the anteterminal stripe of both wings. Some specimens collected during the same month (July) in the same locality (Kafakumba, Upper Lomami, Katanga) even differ widely amongst themselves in the underside ground colour. It is not certain, therefore, that *hollandi* is a true geographical subspecies and I treat it only provisionally as such ; however, I have never seen *hollandi* from Western Africa (Sierra Leone, Liberia, Ivory Coast, etc.).

Aphnaeus orcas ♀ f. *overlaeti* Berger.

A. orcas ♀ f. *overlaeti* Berger, 1952, *Lambillionea* 52 : 70.

Differs from the typical form in the upperside of both wings : instead of being of a uniform blackish-brown tinge, it is invaded by light fulvous, on the fore wings there remains but a blackish costal and marginal border, on the hind wings a blackish costal and abdominal zone.

Habitat : BELGIAN CONGO : Lualaba, Sandoa, Kapanga ; Tshuapa ; Eala. This seems to be the common form in Lualaba, but very scarce elsewhere.

Aphnaeus orcas ♂ f. *fontainei* Berger.

A. orcas ♂ f. *fontainei* Berger, 1952, *Lambillionea* 52 : 70.

Differs from the typical form in that all the silver stripes on the underside are so much widened that they are only separated by thin dark borders.

Habitat : BELGIAN CONGO : Sankuru, Omotumba.

Aphaneus orcas f. paupera f. n. (Plates I and II, figs. 11 and 12).

Male : Differs from the typical form by the following characters. *Wings, underside.—Fore wing :* Basal spot and silvered stripes as in the typical form, but the basal spots reduced to a dot and the stripes much less wide, their dark red borders thick and very strongly marked. *Hind wing :* Sub-basal silvered stripe divided into two confluent spots : one between 8 and the upper edge of the cell, the other in the cell ; the wide discal stripe of the typical form is replaced by narrow spots, one covering the discoidals, the others situated a little beyond, towards the marginal border : one, irregular between 8 and 6, four small and confluent between 6 and 2 ; all the silvered markings of hind wing widely encircled with dark red ; anteterminal stripe dark red, thick and very obvious, encircling only a few silver scales. The reduced size of all the silvery markings give to the underside of both wings a general appearance that is very different from that of the typical form.

Female : All the silvered markings reduced as in the male.

Holotype male : Lulua, Sankuru, Upper Kasai, *Landbeck*, 1902. 4 leg., ex coll. Oberthür, in British Museum (Nat. Hist.).

Allotype female : UGANDA, between Seziwa River and Kampala, 3500 ft.-3750 ft., 27–31.viii.1911 (*S. A. Neave*), in British Museum (Nat. Hist.).

Aphnaeus argyrocyclus Holland (Text-fig. 3).

A. argyrocyclus Holland, 1890, *Psyche, Camb. Mass.* 5 : 431 ; 1893, *Ent. News* 4, pl. i, fig. 15.
A. propinquus Holland, 1893, *Ent. News* 4 : 25, pl. i, fig. 14.

There is no doubt that *propinquus* is the male corresponding to the female described earlier as *argyrocyclus*. This species can be easily separated from *orcas* by the *underside* markings, the subapical silvered stripe of fore wing being broken into spots, the discal band of hind wing being much less wide and somewhat irregular.

The *upperside* of wings of the female is liable to some variation : in a specimen from Bitje, Ja River, Cameroons, it is wholly blackish-brown, without any blue reflection, the discoidal patch is small and the subapical series of dots is obsolete, the anal lobe is tinged with red.

Male genital armature : Slide no. 3202, Etoumbi, Middle French Congo. Of the normal *Aphnaeus* type, the valvae very oblong.

Habitat : Upper waters of the River Ogowe (type) ; GABOON : Manila. MIDDLE FRENCH CONGO : Etoumbi. CAMEROONS : Bitje, Ja River. BELGIAN CONGO. Maniema : Kindu. UGANDA : Toro, Kampala (*van Someren*).

Aphnaeus nyanzae sp. n. (Text-figs. 4 and 18),*

Male : Frons covered with reddish-brown hairs, a small median tuft of white hairs. Eyes encircled with white scales. Second joint of palpi blackish above, whitish below, third joint blackish. Antennae blackish, the last four segments of the club white. Thorax clothed above with bluish-grey hairs. Legs covered with white hairs and scales.

Wings, upperside.—Fore wing : Black with a large triangular shining violet-blue spot, stretching from the cell to the internal border, the outer edge of this spot longitudinally crosses the cell (where it is rather diffuse), runs along vein 4, then parallel to the external border up to the internal border, so leaving a black marginal border about 2 mm. wide, the veins crossing this spot underlined with black ; some violet-blue scales on the discoidals and between veins 6 and 4. Fringe blackish at the base, whitish in the distal half. *Hind wing :* Black with a triangular shining violet-blue spot between the cell end and veins 6 and 2, leaving a black marginal border which is 3 mm. wide at the level of 6, 1·5 mm. at the level of 2, the veins crossing the spot underlined with black ; long silky hairs along 1*b* ; abdominal border light bronze up to 1*b* ; some carmine scales in the lobe and between the extremities of 2 and 1*b* ; two fine black, white-tipped tails at the ends of 2 and 1*b*, the last with some orange scales at its base. Fringe whitish, chequered with black at the ends of the veins, lobe bordered with long black scales. *Wings, underside :* Light reddish brown with numerous silvered spots encircled with a ferruginous edge. *Fore wing :* A small round spot in the cell base, a transverse one in its middle, a transverse one covers the discoidals, a small dot between 7 and 10, a stripe of confluent postdiscal spots from 7 to 2, one oblique spot between 2 and 1, less brilliant than the others, a submarginal series of small internervural dots from 7 to 2, the first two silvered, the others reduced to some blackish scales ; shining yellowish-brown area along the internal border and thin black marginal line. *Hind wing :* Two small basal spots, one at the base of the costa, the other at the base of the abdominal border ; a small round spot in the cell base, a small dot on 1*b* ; a large round spot between 8 and 7, confluent with an oblong one which covers the discoidals ; a postdiscal series of spots, viz. : three confluent between 7 and 4, one irregular in shape confluent with the discoidal spot, one isolated on 1*b*, one oblique between 1*b* and 1*c* ; anteterminal dark red line, parallel to the marginal border, a silvered streak between 1*b* and the abdominal border ; some carmine, orange and silvered scales near the end of 1*b* ; a thin black marginal line. Fringe as above. Expanse : 28 mm.

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* See p. 516. Received after preparation of Blocks 1–17.

Male genital armature : Slide no. 3914, Katera. Of the usual *Aphnaeus* type ; the valvae are like those of *orcas*, but the penis is of the *argyrocyclus* type.

Holotype male : UGANDA : Katera, Sango Bay, xi. 1953 (*T. H. E. Jackson*), in coll. T. H. E. Jackson.

Female unknown.

A. nyanzae evidently belongs to the *orcas-argyrocyclus* group, but it can be separated from these two species at a glance by the colour of the upperside spots which are shining violet-blue instead of brilliant, almost metallic greenish-blue as they are in specimens of *orcas* and *argyrocyclus* from all localities ; the disposition of the silvered spots on the underside and the genitalia also are different in the three species referred to above.

A. nyanzae was collected together with numerous specimens of *A. orcas hollandi* Butler.

Aphnaeus asterius Plötz (Text-fig. 5).

A. asterius Plötz, 1880, *Stettin. ent. Ztg.* **41** : 201.

The rather short original description runs as follows :

> 166. *Aphnaeus Asterius* n. sp. Aburi, 22 September 1872, 1 ♂. Vdfl. 20 mm. Die Oberseite ist dunkelbraun mit blauem Anflug, die Unterseite der Flugel braungelb mit vielen kleinen braun eingefassten Silberflecken : auf den Vdfln. sind 12 und ein langer Streifen gegen den Hinterrand, auf den Htfln. sind 18 zum Teil quer oder längs stehende Fleckchen und ein schwarzer vor dem Vorderwinkel. Nur an Rippe 1 sehe ich ein langes Schwänzchen.

As to the colour of the underside, this description cannot be applied to any male of the *asterius* group, for in all the specimens of this sex that I have examined, the underside is always of a carmine-brown tint, very dark, almost violaceous. But, as will be seen, the underside colour of the female varies from light chestnut to light brownish-yellow and deep orange-yellow. It seems to me very probable that the holotype of *asterius* was, in fact, a female and not a male. Such errors of description were not rare among authors of the 19th century. Unfortunately, I cannot give any decisive proof supporting this opinion, the type not having been traced in the Greifswald Museum where it was placed, according to the note by Aurivillius in *Rhopalocera Aethiopica* : 328.

I believe that the male of the species described by Plötz is *Aphnaeus chalybeatus* E. Sharpe, 1890 (*Ann. Mag. nat. Hist.* (6) **6** : 105 ; 1890, *Trans. ent. Soc. Lond.* **1890** : 555, pl. 18, fig. 7). This was also the opinion of Aurivillius, who treated *chalybeatus* as a synonym of *asterius*. Miss Sharpe's description being very short, I think it is well to give another one, based on the type in the British Museum (Nat. Hist.).

Male : Frons covered with blackish hair, a small median tuft of carmine hair and another of white hair between the base of the antennae. Eyes encircled with white scales. Second joint of the palpi blackish above, orange beneath ; third joint blackish. Antennae blackish, the tip of the club pale yellow. Thorax black above, furnished below with reddish hair.

Wings, upperside : Deep black with patches of brilliant greenish-blue scales disposed as follows. *Fore wing :* In the basal half of the cell, on the discoidals, between the veins in the postdiscal zone and between 3 and the internal border, but nowhere reaching either the external border or the tornus. Blackish fringe. *Hind wing :* Greenish-blue subtriangular area between 5 and 2, not reaching the marginal border. Costal and abdominal areas bronze-black, vein 1*b* underlined with long hair, tails long and slender, black, white-tipped, at the ends of veins 2 and 1*b*. Fringe blackish, whitish between 2 and the lobe which is bordered with long black scales. *Underside :* Carmine-brown with numerous very shiny silver dots or streaks disposed as follows : *Fore wing :* A dot at the base of cell, two placed one above another in the middle of cell ; two small streaks covering the discoidals, a very irregular postdiscal series of five dots : one very small between 10 and 7, one much displaced towards the external border between 7 and 6, one between 6 and 5 in line with the first, an oval dot between 5 and 4, much displaced towards the external border, a small dot between 4 and 3, in line with the first and third, a small subapical dot between 7 and 6 ; a light area, slightly silvered in its upper part, between 2 and the internal border, bordered with black and which does not reach the external border. Fringe as above. *Hind wing :* Three sub-basal dots : in the base of cell, between 2 and 1*b* and at the base of the abdominal border ; a narrow streak on the discoidals , a very irregular post-discal series of six dots : between 8 and 7, 6 and 5, 5 and 4, 4 and 3, 3 and 2 and, above the lobe, a long streak directed towards the base of the abdominal border ; two small dots above the lobe, followed by a streak parallel to the postdiscal one ; lobe black, dusted with silver scales. Fringes as above. Expanse : 29 mm.

Habitat : "SIERRA LEONE."

Among the males that I could examine, I have observed the following variation. The upperside blue patches may be greenish, as in the type of *chalybeatus* and in 1 ♂ Sierra Leone, ex coll. Crowley, 1 ♂ Sierra Leone ex coll. Bethune-Baker, 1 ♂ without locality label, ex coll. Joicey, in the British Museum (Nat. Hist.) and 4 ♂ Eala (near Coquilhatville), Belgian Congo (*J. Ghesquiere*) in the Musée du Congo Belge, of Tervuren ; or they may be slightly violet as in 2 ♂ Bitje, 2000 ft., wet season (*G. L. Bates*) and 1 ♂ Gaboon, ex coll. Crowley, also in the British Museum. In this connection it is worth noting that in the specimen figured on the plate in the *Trans. ent. Soc. Lond.* **1890**, the tint is more violet-blue than greenish-blue, so that we may suppose that the specimen from Gaboon was taken as the model.

On the underside some of the silver dots are occasionally lacking, sometimes there are extra dots ; for instance in the postdiscal series on the fore wings, between 3 and 2 or in the submarginal area ; a rather common form shows a lengthening of the postdiscal spot situated between 5 and 4 so as to form a streak ; in extreme specimens, this streak nearly reaches the external border (1 ex Gaboon, 1 ex Bitje, 1 ex Eala). Holland considered this last form as a distinct species, described it under the name *argenteola* in *Psyche* **5** : 430 (1890) and figured it in *Ent. News* **4**, pl. i, fig. 12 (1893). I cannot accept this view for all the intermediates between the oval dot and the complete streak can be observed. Moreover, the tint of the underside remains constantly deep carmine brown in all the specimens.

Male genital armature : Slide no. 3238, Sierra Leone. Of the type common to *Aphnaeus*, the penis of a reduced size, compared to the whole genitalia, the inferior process of valvae very long. Among the females studied, I was able to separate three distinct forms : *Form A* : Nearest to the description of *asterius* given by Plötz. I give below a more complete description of it, based on a specimen from Eala (Belgian Congo) :

Forehead, eyes, palpi, antennae and thorax as in the male of *chalybeatus* described above.

Wings, upperside : Blackish-brown dusted with violet-blue scales as follows : *Fore wing :* End of the cell, discal zone, more densely between 2 and 1. *Hind wing :* discal area, between 5 and 2. Lobe black, dusted with white scales and bordered with long black and white scales. Two long and slender tails, blackish, white tipped. Blackish fringe. *Underside :* Yellow-orange ochreous, of a rich and warm tint, with silver markings encircled with black scales, disposed as follows : *Fore wing :* A dot at the cell base, two in its middle, two on the discoidals, postdiscal series composed of six dots : one between 10 and 7, one displaced towards the external border between 7 and 6, one in line with the first between 6 and 5, one very oval in shape and much displaced towards the external border between 5 and 4, two disposed one above the other between 4 and 3, 3 and 2, a very small subapical spot ; a wide light scaly area, silvery in its upper part, between 2 and the internal border. *Hind wing :* Four small sub-basal dots : one under 8, one in the cell, one upon 1*b*, one at the abdominal border ; a streak on the discoidals ; an irregular postdiscal series of seven dots between 8 and 1*b* and a long streak directed towards the wing base between 1*b* and the abdominal border ; above the lobe, a second streak parallel to the postdiscal one ; lobe black, dusted with silver scales. Fringe as above. Expanse : 31 mm.

Very likely it is this form that Holland described as a distinct species under the name of *ilogo* in *Psyche* (**5** : 429, 1890) and figured in *Ent. News* (**4**, pl. i, fig. 11, 1893). Holland took his *ilogo* type for a male, but from the above cited figure, it is easy to see that it is, in fact, a female, the shape of the wings being very different in the two sexes. Holland described the underside colour as " deep cadmium orange " and this corresponds well with my Eala specimen.

Among the females of Form A that I examined, I have noted the following variations : the density of the violet-blue scales on the upperside varies from one specimen to another. On the underside, the ground-colour is deep orange yellow ochreous in five specimens : 2 ♀ Eala and 1 ♀ Katako Kombe, Sankuru, Belgian Congo, in the Belgian Congo Museum ; 1 ♀ Sierra Leone, ex coll. Crowley and 1 ♀ Sierra Leone, ex coll. Adams in the British Museum (Nat. Hist.), and light yellowish-brown in five others : 1 ♀ W. Africa, 1 ♀ Ivory Coast, ex coll. Oberthur, 1 ♀ Bitje, April, Bates leg., 2 ♀ Bitje, April–May, ex coll. Adams, all in the British Museum (Nat. Hist.).

The number of silver dots on the underside is very variable. The Eala specimen described above matches in this respect Holland's figure of *ilogo*, but in another specimen from the same locality the dots on the hind wing underside are much reduced in number and size.

Form B : Described from a female from Bitje, April, Bates leg., ex coll. Joicey, in British Museum (Nat. Hist.).

Frons, eyes, palpi and antennae as in form A. *Wings,—upperside :* As in form A. *Underside :* Ground colour light chestnut with silver dots and streaks, widely encircled with black scales, very brilliant and a little larger than in form A. *Fore wing :* As in form A but, in addition, an anteterminal series of five dots : one very small between 8 and 7, one larger below the first between 7 and 6, one displaced towards the external border between 6 and 5, one very small between 5 and 4, one small between 3 and 2, some black scales between 2 and 1 ; a very narrow black marginal line. Fringe blackish. *Hind wing :* As in form A, but some carmine scales are mixed with the black ones which encircle the first two sub-basal dots, also one anteterminal dot between 7 and 6 and two dots above the lobe ; narrow black marginal line. Fringe rufous from the apex to 6, blackish chequered with white from 6 to 2, white from 2 to the lobe. Expanse : 29 mm.

Another specimen from Bitje, October, 1909, ex coll. Adams, in British Museum (Nat. Hist.), matches this description. In two others from Bitje

(1 ♀ wet season ex coll. Joicey, 1 ♀ November, 1909 ex coll. Joicey, both in British Museum) the chestnut colour of the underside is shaded with yellow.

Form C : Described from a specimen from Bitje, 2000 ft., dry season (*G. L. Bates*), ex coll. Joicey, in British Museum (Nat. Hist.).

Frons, eyes, palpi and antennae as in forms A and B.

Wings, upperside : Blackish brown with a slight russet reflection, chiefly in fore wings, between 3 and the internal border. No blue scales. *Hind wing :* Costal and abdominal areas bronze blackish, the base of the tail at 1*b* orange. Fore wing fringe blackish, hind wing fringe pale rufous between the apex and 6, grey mixed with white between 6 and 2, white between 2 and the lobe which is bordered with long black scales. *Underside :* Vivid orange-yellow with shining silver dots, disposed as in the form B, but very reduced in size,

Of this form I have also seen the following specimens : 1 ♀ Bitje, dry season, ex coll. Druce-Joicey; 1 ♀ Bitje Oct.–November, ex coll. Joicey, 1 ♀ Bitje. wet season, x.1909, ex coll. Adams, 1 ♀ Bitje, wet season, xi.1909, ex coll. Adams, all in British Museum (Nat. Hist.).

It is this form that Bethune-Baker described as the female of *chalybeatus* (1926, *Ann. Mag. nat. Hist.* (9) **17** : 398) from a specimen from Bitje. I have examined it and noticed that on the discoidals, on the upperside, there are two small, light-blue, shining dots, not mentioned in Bethune Baker's description, and that the underside tint is vivid chrome yellow rather than orange yellow. Finally, I must admit that, in spite of the relative richness of the material examined, I have been unable to convince myself as to whether only one, two or perhaps more species are represented in it. It is true that the three female forms differ noticeably and that all three are found at Bitje, the only station from which we have many specimens. They cannot be geographical races, and besides, they are not seasonal forms since the form C was collected in both dry and wet seasons. Yet, I have failed to find any constant character justifying the separation into two specific units in the males, the differences in the upperside tinge, whether greenish-blue or violet-blue, are slight and may merely indicate the degree of freshness or the method of relaxing before setting. Amongst the females, the density of blue scales of the upperside is very variable as also are the number and size of the silver spots and the underside ground colour with its two extreme forms, light chestnut and vivid orange-yellow. I think that the point can be decided only after the study of much more material from many different localities.

Aphnaeus questiauxi Aurivillius (Plates I and II, fig. 16, and Text-fig. 6).

A. questiauxi Aurivillius, 1903, *Ark. Zool.* **1** : 252, fig. 6.

In his text, Aurivillius did not mention the sex of his type, but from the description and figure we may infer that it is a male. The female was later described and figured by Neave (*Proc. zool. Soc. Lond.* **1910** : 48, pl. ii, fig. 4.)

Male genital armature : Slide no. 3239, Sontola River, Luena district, N.E. Rhodesia. Of the usual *Aphnaeus* type, the upper process of the valvae slender, the lower process triangular, the penis rather long.

Habitat : BELGIAN CONGO : Katanga, Kapanga, river Kutshindji. N.E. RHODESIA: Luena district, Alala plateau near Broken Hill, Kalungwisi Valley, Lake Bangweolo district.

Aphnaeus brahami Lathy (Text-fig. 7).

A. brahami Lathy, 1903, *Trans. ent. Soc. Lond.* **1903** : 199, pl. viii, fig. 10.

Male (hitherto undescribed, Lathy's text does not mention the sex, but the holotype is a female labelled Ogruge, Nigeria.) Vertex furnished with dark carmine-red hair ; frons with light rufous hair, two white lateral lines. External side of eyes edged with silver scales. Second joint of palpi white, third joint blackish. Antennae brown with some white scales, tip of the club pale yellow. Thorax above covered with blue scales, furnished beneath with whitish hair, abdomen blackish annulated with white.

Wings, upperside : Blackish-brown with vivid violet-blue areas, disposed as follows : *Fore wing :* A small stria at the base of cell, a small dot in its middle, one upon the discoidals, a large area stretching between the lower border of the cell, vein 2 and the internal border, from the wing base up to about 2 mm. from the tornus ; marginal line blackish, thin. Fringe brown at the base, white in its distal half, chequered with blackish at the ends of the veins. *Hind wing :* A large vivid violet-blue patch covering the cell and the discal area between 6 and 2, the external border of this patch evenly curved, nearly reaching the marginal border at the level of 2 , costal area bronze-brown ; abdominal area light yellowish-grey covered, like the cell, with long silky hairs ; a slender and short tail black at the end of 2 ; a long slender tail at the extremity of 1*b*, dark red at the base, white at the tip ; a very thin marginal line. Fringe as in fore wing. *Underside :* Light yellowish-grey brown with numerous shining silver spots encircled with dark red and some black scales, disposed as follows. *Fore wing :* A basal spot between the costa and 12, contiguous to a round spot in the cell base ; an oblong spot, beginning very near the costa, crosses the middle of cell and nearly reaches the origin of 2 ; an oblong spot beginning on 12, covers the discoidals and the base of the interspace between 4 and 3 ; postdiscal series of eight spots : four confluent between 11 and 10, 10 and 7, 7 and 6, 6 and 5, one sharply displaced towards the external border between 5 and 4, two confluent figure 8-shaped, between 4 and 3, 3 and 2, in line with the first four, an oblique oval spot between 2 and 1, a small anteterminal spot between 7 and 6; area stretching from the lower border of the cell to the internal border sealy, shining, lighter than the other parts of the wing ; submarginal line dark red, very thin. Fringe white, chequered with white at the ends of the veins. *Hind wing :* Two basal spots, one at the beginning of the costa, the other very small, at the beginning of the abdominal border ; four sub-basal spots, one large, rounded, between the base of 8 and the upper border of the cell, one small in the cell base, one stria-shaped on 1*b*, one small between 1*b* and the abdominal border ; a large quadrate spot on the discoidals ; postdiscal series of nine spots ; one large, oval, between the costa and 7, above the discoidals, six smaller, in irregular-line, between 7 and 1*b* ; one on 1*b*, one elongate, obliquely placed between 1*b* and 1*a* ; a silver stria above the lobe ; antemarginal stripe dark reddish, mixed with black scales, diffuse, parallel to the marginal border ; in the lobe a black ocellus encircled with carmine ; marginal line dark red, very thin ; tails as above. Fringe whitish. Expanse : 33 mm.

Neallotype : DAHOMEY, near Porto Novo, (*Waterlot*), 1909 leg. In Muséum National d'Histoire naturelle, Paris.

A male in my collection—unluckily with an unrecognizable locality label "Couba"—only differs from the neallotype by the presence, on the fore wing underside, of a second small anteterminal silver spot between 8 and 7. But I have been able to examine, in the British Museum, another male from M'Pala, Tanganyika, which differs from the preceding ones by the following characters :

Wings, underside : Light violaceous-brown, washed with light-yellowish in hind wings ; all the silver spots much larger, encircled with black scales ; there are also additional spots as follows : *Fore wing :* An anteterminal series of seven spots : three confluent between 9 and 6, four isolated between 6 and 2. *Hind wing :* Two small anteterminal spots, widely encircled with black between 8 and 6 ; marginal line of both wings blackish instead of dark red. This form may be peculiar to the eastern parts of the species range.

Male genital armature : Slide no. 1855, near Porto Novo, of the general *Aphnaeus* type.

In the female holotype described and figured by Lathy, the ground-colour of the underside is rather dark brownish-grey, all the silver spots are reduced in size and some on the fore wing are lacking, but this form is perhaps only individual.

Habitat : DAHOMEY, NIGERIA, TANGANYIKA.

Aphnaeus jefferyi Hawker Smith (Text-fig. 8).

A. jefferyi **Hawker Smith, 1928, *Bull. Hill Mus.* 2 : 30.**

Male (hitherto undescribed) : Frons covered with bronze and pale grey hair, with two white lateral lines. Second joint of palpi greyish-white, third joint brown. Antennae (lacking in the described specimen) : Thorax covered above with long silky hair, beneath with grey hair.

Wings, upperside : Blackish-brown with the following pattern : *Fore wing* dusted with greenish-blue shining scales on the lower half of the cell and the basal part of the interspaces between 4 and the internal border, the outer limit of this dusted area evenly curved, the blackish-brown marginal area about 4–5 mm. wide at the level of 4, 3 mm. at the tornus. *Hind wing :* Costal area bronzed brown up to 6 ; part of the cell and interspaces between 6 and 2 dusted with greenish-blue scales, the outer edge of this dusted area oblique to the marginal border from which it is distant about 5 mm. at the level of 6, 1 mm. at the level of 1 ; lobe reddish-brown ; a slender and short tail, black, white tipped, at the end of 2 ; a similar tail, but much longer, at the end of 1*b* ; abdominal border light bronzed brown ; long silky hairs cover a part of the cell and run along 1*b*. Fringe of both wings brown at the base, lighter in its distal half. *Underside :* Yellowish-brown, slightly orange, with numerous silver spots encircled with black or carmine-red scales. *Fore wing :* A small round spot, encircled with black in the base of cell, an oblong spot from 12 to the rear of 2, so crossing the middle of cell, encircled with red scales in its upper part, with black scales in its lower part ; an oblong spot, encircled with red, covering the discoidals and reaching the beginning of 3 ; postdiscal series composed of three small confluent spots encircled with red scales, between 10 and 7, 7 and 6, 6 and 5 ; a small stria encircled with black and red scales sharply displaced outwards between 5 and 4, a spot encircled with black and red scales between 4 and 3, in line with the first three, a spot widely encircled with black scales between 3 and 2 and finally an oblique stria between 3 and 2 ; black dot encircled with red scales between 7 and 6, below the origin of 8 ; between the lower edge of the cell, vein 2 and the internal border a scaly and shining area ; marginal line reddish, rather wide. *Hind wing :* A basal round silver spot, encircled with black and red scales at the beginning of the costa, four sub-basal spots, namely a silver one encircled with black and red scales, between the origin of 8 and the upper edge of the cell, a black, indistinct one in the cell, a silver one on 1*b* and another on the abdominal border ; a large sub-rectangular silver spot on the discoidals, edged with black proximally, red distally ; postdiscal series composed of a large silver spot between 8 and 7, edged with red inwardly, with black outwardly, three small dots reduced to some silvered scales widely encircled with black between 7 and 4, four small silver spots encircled with red between 4 and 3, 3 and 2, 2 and 1*b* and on 1*b* and finally an oblique silver stria edged with black and red scales from 1*b* to 1*a* ; submarginal stripe diffuse, slightly obscure, containing some black scales between 7 and 6 ; some black and silver scales above the lobe ; lobe reddish with some white scales ; marginal line reddish, rather wide. Fringe of fore wings as above, of hind wings lighter. Expanse : 32 mm.

Male genital armature : Slide no. 3411, Soy, Kenya. Of the normal *Aphnaeus* type, but the penis less massive, more elongated than in the other species.

Neallotype : KENYA ; Soy, 2.v.1929 (*C. Cripps*), in British Museum (Nat. Hist.).

In the female, the powdering of metallic scales is blue instead of greenish-blue, it is also less extended ; the underside ground colour is of a deeper tone than in the male, the pattern is the same, but the spots are light yellowish.

Habitat : KENYA.

Aphnaeus erikssoni Trimen (Plates I and II, fig. 8, and Text-fig. 9).

A. erikssoni Trimen, 1891 (♀), *Proc. zool. Soc. Lond.* **1891** : 86, pl. ix, fig. 15.
A. bruneeli Berger, 1951, *Rev. Zool.-bot. Afr.* **45** : 55.

Trimen's original description is based on a unique female, collected at Ehanda, South Ambuella, Mossamedes district ; it is very complete and can be summarized as follows :

Wings, upperside : Dull brownish-red. *Fore wings :* A small square yellow-ochreous spot, at the end of the cell ; a postdiscal series of five small spots of the same colour, of which the third is displaced towards the external border. *Hind wing :* Traces of three indistinct yellow ochreous spots, one discoidal, two postdiscal ; anal angle much produced with trace of a tail at the end of 2 ; fulvous lobe sprinkled with greenish-bronze scales. *Underside :* Brownish-yellow ochreous with large yellow ochreous spots of a lighter tint than that of the ground, encircled with ferruginous-brown. *Fore wing :* Two spots in the cell, one at its end ; postdiscal series of six confluent spots of which the third is displaced towards the external border, the sixth (between 2 and 1) displaced towards the base ; seven antemarginal spots. *Hind wing :* Four sub-basal spots, the second in the cell, the third farther from the base than the preceding one, large discoidal spot ; postdiscal series of nine confluent spots ; antemarginal series of six spots ; some metallic green scales in the lobe. Expanse : 35–36 mm.

In the British Museum and the Oxford Museum, are three females which agree with this description. These have the following data : (1) N.W. RHODESIA: Kabombo River, Pokala Rapids (*C. M. N. White*) (Oxford Mus.). (2) KATANGA ; TANGANYIKA : M'pala, (Brit. Mus. (Nat. Hist.)). However, the colour of the upperside is more orange-red than dull brownish-red, but Trimen's specimen is rather worn.

The males from N.W. Rhodesia and Katanga which seem to belong to the same race as the above cited females, differ widely from those from Mashonaland, further described by Trimen. I was able to examine the following specimens : 3 ♂ N.W. RHODESIA : Kabombo River, Pokala Rapids (*C. M. N. White*). 1 ♂ N.W. RHODESIA (*H. Cookson*). 2 ♂ N.W. RHODESIA: Kukanga. 4 ♂ KATANGA. 1 ♂ KATANGA : Mutendale River, near Lualaba River (*H. Cookson*), all in Brit. Mus. (Nat. Hist.). 1 ♂, N.W. RHODESIA : Alala Plateau, Mkushi district, 4000 ft. (*Neave*) Oxford Mus. A long series (about 40 ex), KATANGA, most of them from Kafakumba, Upper Lomami, in Belgian Congo Museum. The facies of all these males can be described as follows :

Frons, palpi and antennae as in the female. *Wings, upperside :* Uniform orange-red like the female, in two specimens only (Lukanga and Alala Plateau), a very slight blue suffusion at the base of fore wings, reduced to the space between vein 1 and the internal border ; discoidal and postdiscal spots of fore wing as in the female, the same spots lacking on the hind wings in some specimens ; brown diffuse marginal border on both wings. *Underside :* Like that of the female, with large confluent yellow ochreous spots. Expanse : 32–34 mm.

All these specimens seem to me to belong to the nominal race which would then inhabit Southern Angola, N.W. Rhodesia, Katanga and, so far as I can judge from a unique example, the M'Pala region. The males of this race are so different from Trimen's male *erikssoni* that Dr. Berger, considering them a distinct species, named them *bruneeli*.

I select as male neallotype of *erikssoni erikssoni* the male no. 3247 from Katanga (Brit. Mus. (Nat. Hist.)), the female holotype being, of course, the specimen from Southern Angola, described by Trimen, in 1891.

Male genital armature: Slide no. 2662, Kafakumba, Katanga. Of the type common to all *Aphnaeus* species, the anterior edge of the dorsum shows a small median projection; the very thick penis contains a big cuneus with a serrated edge; the vesica is furnished with several rows of long and fine spines.

A. erikssoni mashunae subsp. n.

A. erikssoni ♂ Trimen, 1898, *Trans. ent. Soc. Lond.* **1898** : 9, pl. i, fig. 5.

Differs from the nominate race in the following characters:

Male wings, upperside.—Fore wing: Orange-red with a shining light blue area between the cell and the internal border, the upper edge of this blue area follows the lower edge of cell up to the origin of vein 2, then obliquely crosses the space between 2 and 1 and reaches the internal border at 4 or 5 mm. from the tornus; discoidal and post-discal spots yellow ochreous as in the nominal race. *Hind wing:* Orange-red with a very slight blue suffusion at the base; discoidal and postdiscal spots often reduced or even absent; blackish diffuse marginal border on both wings. *Underside:* Brownish-yellow ochreous with large yellow ochreous spots as in the nominal race; those of the postdiscal series of both wings confluent, those of anteterminal series of fore wings sometimes indistinct. Expanse: 32–34 mm.

Male genital armature: Identical with that of the nominate race.

Male holotype: Mashonaland: Gadzima, Umfuli River (*G. A. K. Marshall*) (described and figured by Trimen *loc. cit.* 1898), British Museum (Nat. Hist.). Paratypes: 2 ♂ from the same locality, cited by Trimen, 1 ♂ same locality, ex coll. H. H. Druce, 1 ♂ N. Rhodesia: Chinundas Village; all 4 paratypes in British Museum (Nat. Hist.).

One male from Chintechi, Nyasaland, in the British Museum, is very near the Mashonaland race, but the blue spot on the fore wing is a little less distinct. One male from Druid Mine, Pilabusi, 4500 ft., S.W. Rhodesia (*E. Lannin*), in T. H. E. Jackson collection is like *mashunae* above, but of a darker, less orange red; also the reduced size of the underside spots and the absence of the anteterminal series make it near the race *barnesi*, described below.

Unfortunately, I could not examine females from Mashonaland; this sex seems to be much more rare and is lacking in the collections available to me.

Aphnaeus erikssoni barnesi subsp. n. (Plates I and II, fig. 1).

Differs from the nominal race in the following characters:

Male wings, upperside.—Fore wing: Carmine-red and not orange-red; basal vivid blue area between the cell and the internal border larger than in *erikssoni mashunae*, its upper edge following the lower border of cell, the basal half of 2, then obliquely crossing the space between 2 and 1 to rejoin the internal border 2 or 3 mm. from the tornus; sometimes the blue tinge slightly invading the base of cell; discoidal and postdiscal spots sometimes yellow ochreous (in 2 specimens) but more often of a bluish-white, neatly encircled with black; marginal band blackish, more distinct than in the preceding races. *Hind wing:* Carmine-red, the base washed with blue; the discoidal and postdiscal spots reduced or absent, when present, they are blue and not yellow ochreous; marginal band blackish, diffuse and indistinct. *Underside:* Ground colour reddish-brown with yellowish-brown spots encircled with dark brown, much smaller than in the preceding races, generally reduced to the size of dots; the fore wing anteterminal series completely absent. Expanse: 30–34 mm.

Male genital armature: Identical to that of the nominate race.

Female wings, upperside.—Fore wing: Carmine-red, basal vivid blue as large as in the male, discoidal and postdiscal spots bluish-white, marginal band blackish, distinct. *Hind wing:* Carmine-red, widely washed with blue at the base and on the disc; postdiscal spots very small, bluish. *Underside:* As in the male. Expanse: 35–38 mm.

Male holotype: S. Rhodesia: Christmas Pass, 4000 ft., near Umtali. Specimen no. 3210 (*E. W. Lannin*), T. H. E. Jackson coll.

Female allotype: S. Rhodesia: Umtali (*B. D. Barnes*), Stempffer coll.

Paratypes: 1 ♂ S. Rhodesia: Bindura, 3500 ft. (*T. H. E. Jackson*); 3 ♂ Christmas Pass (*E. W. Lannin*), T. H. E. Jackson coll.; 5 ♂ Umtali (*B. D. Barnes*), Stempffer coll.; 1 ♂ Umtali, 18.x.24 (*E. W. Lannin*), Brit. Mus. (Nat. Hist.). A fine series of 22 ♂, 1 ♀, collected by B. D. Barnes on the Vumba Mountains, 5000 ft. (near Umtali, on the Mozambique border) shows an intermediate facies between *barnesi* and *rex* Aurivillius, some specimens having the underside postdiscal spots metallic green near the abdominal border. Another male, from Vumba, certainly aberrant, deserves a special description. It is above, reddish-brown instead of carmine-red; the blue area of the fore wings is reduced in size, the postdiscal spots are absent; the costal border of hind wings is blackish up to 6; the underside is yellowish-brown, all the pattern having disappeared except for the postdiscal spots near the abdominal border. E. C. Pinhey (1949, *Butterflies of Rhodesia*: 104) has already pointed out the existence of this individual form. The male specimen figured by E. C. Pinhey (*loc. cit.* pl. xiii, fig. 7) seems to belong to the subsp. *barnesi*.

The presence of two distinct races of *erikssoni* in Southern Rhodesia may be explained by the differences of climate within the country. B. D. Barnes has been so kind as to inform me that the average annual rainfall at Gadzima is 32 inches, at Pilabusi 25 inches, Christmas Pass 35 inches, Bindura 32 inches and Vumba 65 inches. While *erikssoni mashunae* occurs within the large upland, *erikssoni barnesi* is found on its eastern edge, which rises above the plains of Portuguese East Africa. This slope is exposed to the wet winds coming from the Indian Ocean. Whilst at Bindura the Mazee River flows gradually towards the Zambezi valley, the Vumba Mountains, on the other hand, overlook the Mozambique situated 4000 ft. below and the rainfall is heavy and the flora characteristic.

Two males recently received from Eshowe, N. Natal, are very near the Vumba form.

Aphnaeus erikssoni rex Aurivillius, (Plates I and II, fig. 2).

A. rex Aurivillius, 1909, *Ark. Zool.* **5** (5): 5, 6, fig. 41, ♀.

Aurivillius described *rex* from a female from Kigonsera (east of the northern end of Lake Nyasa). I have been able to examine a female from Mlanje, 2300 ft., Nyasaland (*S. A. Neave*), Brit. Mus. (Nat. Hist.), which differs only slightly from Aurivillius' description and figure, in the following particulars :

Wings, upperside.—Fore wing : Discoidal spot pure white instead of light yellow ochreous, postdiscal spots absent. *Hind wing :* Postdiscal spots very reduced, nearly obsolete ; the tail at the end of 2 less slender (perhaps its length has been slightly emphasised in Aurivillius' figure. *Underside.—Fore wing :* Most of postdiscal spots wanting. *Hind wing :* Postdiscal spots between 2 and the abdominal border covered with light green metallic scales.

The following description of the male of *erikkssoni rex* is based on two specimens from Mlanje :

Male.—Frons, palpi and antennae as in the female.

Wings, upperside : Like *erikssoni barnesi*, the postdiscal spots of fore wing very small and bluish-white, encircled with black, those of hindwings lacking, tail at the end of 2 rudimentary. *Underside :* Ground colour reddish-ochreous-brown with spots reduced to the size of dots. *Fore wing :* only five postdiscal spots, those between 2 and the internal border being absent ; those situated between 4 and 3, 3 and 2 are one under the other and not as in Aurivillius's figure ; this last character is therefore variable and cannot be used for separating *rex* from *erikssoni*. *Hind wing :* Postdiscal spots placed between 2 and the abdominal border covered with pale green metallic scales ; submarginal brown line less distinct than in the female, slightly lightened with yellowish near anal angle. Expanse : 29–32 mm.

Male genital armature : Identical to that of the nominate race.

Habitat : NYASALAND.

It may be considered unwise to include in the same specific unit specimens which are, on external appearance, as different as *erikssoni erikssoni* from Katanga and *erikssoni rex* from Nyasaland, the distinctive characters appearing to be numerous and well marked :

	erikssoni erikssoni.	*erikssoni rex.*
Upperside ground colour . .	Wholly orange-red	Carmine-red with a large blue spot.
Discoidal and postdiscal spots .	Yellow ochreous	Bluish white.
Tail at the end of 2 . . .	Rudimentary or absent	Sometimes well developed.
Underside spots	Large, confluent	Very small, separated.
Postdiscal spots between 2 and abdominal border	Yellow ochreous	Metallic pale green.

But these characters are those of the most extreme opposites. If a sufficient number of *erikssoni* from various localities are examined, it will be found that transitional specimens, showing a mixture of characters, are numerous enough ; for instance the blue spot of the fore wing appears as a small suffusion in two *erikssoni erikssoni* from N.W. Rhodesia ; in *erikssoni barnesi*, the postdiscal spots of the upperside are sometimes yellow ochreous, often bluish-white ; finally the metallic green spots of the hind wing underside of *erikssoni rex* appear fairly frequently in the specimens from the Vumba. I believe that, if some hundreds of specimens were available for examination instead of a few dozens, it would be possible to arrange a continuous series of individuals showing a gradual transition from one extreme type to the other. On the other hand, *erikssoni eriksssoni* and *eriksssoni rex* do not seem to fly together anywhere; on the contrary, there seems to be a variation in a continuous direction, coinciding at least generally with the geographical distribution: going from west to east, from the lowlands of Katanga and N.W. Rhodesia to the East African mountains, the colour of the upperside changes from orange-red to carmine-red, the size of the blue area of the fore wing increases, the size of the underside spots is reduced and their number rather diminishes.

The spread of the species over a very wide area has resulted in its division into subspecies, their degrees of differentiation being in direct proportion to their geographical separation; transitional forms occur in the intermediate zones. *A. eriksssoni* seems to me to be a good example of what Mayr has called a "polytypic species."

Aphnaeus affinis Riley (Plates I and II, fig. 6, and Text-fig. 10).

A. affinis Riley, 1921, *Trans. ent. Soc. Lond.* **1921** : 249, pl. vii, fig. 7, 8.

This species, of which the female is not yet known, has some external likeness to *A. eriksssoni eriksssoni* Trimen. However, it can be safely separated by the following details:

	eriksssoni.	*affinis.*
Collar, between head and thorax .	Dark grey to black	Purplish to bronze
Thorax, below	Yellowish	White.
Underside of fore wing. Discal spot between 5 and 4	Strongly displaced towards the outer margin	Less displaced.
Underside of hind wing: First spot of the discal band (between 8 and 7)	Nearer the base than the second spot (between 7 and 6)	Farther from the base than the second spot.

Male genital armature: Slide no. 3237. Chanteti River, Solwezi, N.W. Rhodesia.

Habitat: N.W. RHODESIA: Solwezi; Kabombo River, Iskala rapids. KATANGA; Lupweshi, River Kafakumba.

Aphnaeus affinis seydeli Berger (Plates I and II, fig. 7).

A. affinis seydeli Berger, 1952, *Lambillionea* **52** : 68.

Differs from the nominate form in the following characters:

Male.—Upperside: Ground colour rather variable, running from fulvous to reddish-brown; nearly all veins outlined with black, subapical dots of fore wing of a paler yellow and often encircled with black scales. *Underside:* Ground colour of a deeper violaceous-brown; all ochreous-orange spots very reduced in size and generally isolated instead of being confluent; the anteterminal series quite obsolete in fore wings, very weakly visible in hind wings, between 4 and the anal angle.

Male genital armature: Identical to that of typical *affinis.*

Female (hitherto undescribed): *Upperside:* Vivid reddish-orange brown, much as in the male of *affinis affinis*, marginal border narrow. Fringe whitish, interrupted with light brown at the vein ends. *Underside:* Ground colour as in the male, the ochreous-orange spots disposed as in the male, but smaller. Fringe as above.

Neallotype: N. RHODESIA: Lukanga River, 7.ix.1915, ex coll. Dollman, Brit. Museum (Nat. Hist). This neallotype has been mentioned as a male, both in Riley's description of *affinis* and Berger's description of *seydeli* ; I have verified, by dissection, that it is in fact a female.

Habitat : BELGIAN CONGO : Upper Katanga, Elizabethville. N. RHODESIA: Lukanga River.

Though the general appearance of the underside of *seydeli* is very different from that of *affinis*, I feel convinced that it is but a local race, the size of the underside spots being very variable in *affinis* and indeed throughout the genus *Aphnaeus.*

Aphnaeus marshalli Neave (Text-fig. 11).

A. marshalli Neave, 1910, *Proc. zool. Soc. Lond.* **1910** : 48, pl. ii, fig. 8, ♂.

This species can be easily separated from its allies by the vivid reddish-brown colour of the upperside of the wings and the shining silver isolated spots of the underside. The female differs from the male only in its slightly larger size and in having the discoidal and discal spots of the upperside a little more defined.

Male genital armature : Slide no. 2644, Umtali, S. Rhodesia. Of the type common to the genus.

Habitat : TANGANYIKA PLATEAU : Upper Lofu Valley, Kafue river. SOUTHERN RHODESIA : Mazoe, Mashonaland ; Meikles Jungle, Umtali, Christmas Pass. BELGIAN CONGO : Upper Katanga, Elisabethville.

Aphnaeus neavei Bethune-Baker (Plates I and II, fig. 15, and Text-fig. 12).

A. neavei Bethune-Baker, 1926, *Ann. Mag. nat. Hist.* (9) **17** : 397.

This species has been described from specimens collected at Witu, near the mouth of the Tana River, Kenya. Some specimens from Gaisen and Garissa, Tana Valley, differ somewhat from the type in the following characters :

Wings.—Upperside : Dull brownish-grey with a fulvous sheen. *Fore wing :* A small yellowish indistinct spot in middle of cell. *Underside :* On both wings, a yellowish-brown marginal border, lobe carmine bordered with black and orange yellow scales. Expanse : Much smaller than in the holotype and allotype : ♂ 25–30 mm. (instead of 36), ♀ : 27 mm. (instead of 40).

Male genital armature : Slide no. 3163, Garissa, of the usual *Aphnaeus* type.

Habitat : KENYA : Tana district.

Aphnaeus coronae Talbot (Plates I and II, figs. 13 and 14, and Text-fig. 13).

A. coronae Talbot, 1935, *Ent. mon. Mag.* **71** : 119, pl. ii, fig. 7, pl. iii, fig. 10, ♂.

Described from a unique male collected at Mongalla Station, South Sudan, by Capt. I. G. Owen, June, 1930. Dr. van Someren and Mr. T. H. E. Jackson have recently recorded this species from the Karamoja district, Uganda, where its presence was not suspected.

Female (hitherto undescribed) : externally so like the male that it is advisable to verify the sex by examination of the tarsi of the fore legs. The following characters may, however, be observed : *Wings, upperside.—Fore wing :* The blue dots at the base and middle of cell more developed, nearly confluent ; discoidal spot also larger and bluish white ; upper limit of the blue area of the internal border extends slightly beyond vein 2.

Hind wing: The space between the discal blue spot and the marginal border reddish-brown instead of blackish-brown. *Underside.—Fore wing:* Light zone along internal border a little wider. Expanse: 34 mm.

Neallotype: Uganda: Toror, Karamoja, iv.1950 (*T. H. E. Jackson*), coll. Jackson.

A. coronae f. **vansomereni** f. n. (Plates I and II, fig. 13).

Male wings.—Upperside: Like the nominal form, the blue dots of the discal series of fore wing reduced or even absent. *Underside:* All spots disposed exactly as in typical *coronae*, but instead of being silvery, they are of a plain, dull, light orange tint, with the exception, however, of the obliquely placed spot between 2 and 1 of fore wing and the small stria situated below the origin of 2, which are a little paler and slightly silvery. Expanse: 23–29 mm.

Male genital armature: Slide no. 3242, Labwor Hills, Karamoja. Of the usual *Aphnaeus* type, the anterior edge of the dorsum somewhat sinuate.

Female: Unknown.

Holotype, ♂, Uganda: Labwor Hills, Karamoja, iv.1950 (*Dr. van Someren*), coll. van Someren. Paratype, 1 ♂: Mt. Kadam, Karamoja, iv.1950 (*Dr. van Someren*), coll. van Someren.

The general appearance of the underside of *coronae* f. *vansomereni* is very different from that of the nominate form. Nevertheless, I consider it as an individual form, not a subspecies, for it is found in the same localities and at the same time as *coronae* f. *coronae* Talbot.

Habitat: South Sudan: Mongalla. Uganda: Karamoja district.

Aphnaeus jacksoni sp. n. (Plates I and II, figs. 9, 10, and Text-fig. 14).

Male.—Frons reddish-brown with two white lateral lines. Second joint of palpi clothed with white scales, third joint blackish. Antennae blackish, tip of the club yellowish-white.

Wings, upperside: Blackish-brown with a suffusion of vivid violet-blue scales at the base of fore wings between veins 2 and 1 and along the internal border and on hind wings between veins 4 and 2 and along 1*b*; costal border of hind wing light brown; a short and slender tail at the extremity of 2, black, white tipped; lobe orange bordered with long black scales; abdominal border brown up to 2, clothed with long silky hair. Fringe brown at the base, whitish distally, chequered with brown at the end of veins. *Underside:* Very light chestnut (café-au-lait) with silver spots on fore wings, silver spots and black margins on hind wings only. *Fore wing:* An oval basal spot between the costa and the upper border of the cell; a long spot, nearly touching the costa, crosses the cell and reaches the origin of 2; a large triangular spot based on the costa covers the discoidals and has its apex at the origin of 3; a smaller triangular spot has its base on vein 11, its apex on 5; below this last a small round spot between 4 and 3; anteterminal series of spots formed of two small confluent spots between 8 and 7, 7 and 6, one between 5 and 4, one farther from the external border between 3 and 2, a longitudinal streak between 2 and 1; the basal spot is encircled with black and dark red scales, the longitudinal streak with black scales, all other silver spots with dark red scales; space between 2 and 1 covered with brown scales. *Hind wing:* silver spots: a round one at the base of costa, encircled with black and dark red scales; a long sub-basal spot between the origin of 8 and the upper border of the cell, also encircled with black and dark red scales; a small spot near the base of the abdominal border; discal series composed of an irregular spot from the costa to 7, a large subrectangular spot covering the discoidals, these two last encircled with dark red and a longitudinal streak upon 1*b*; postdiscal series formed of a small stria between

7 and 6, confluent with the first discal spot, a very small spot between 6 and 5, a small one between 4 and 3, one displaced towards the marginal border between 3 and 2, a U-shaped one between 2 and 1*b* and one at the abdominal border, all the spots of the postdiscal series encircled with black and dark red scales. Black markings: a basal spot at the origin of 8, a round spot in the middle of cell with, in its centre, some silvered scales; basal suffusion between 2 and the abdominal border; black spots exteriorly edging the silver markings between 7 and 6, 6 and 5; diffuse black spot, mixed with dark red scales between 5 and 4; anteterminal series of indistinct spots between 7 and 6, 3 and 2, 2 and 1*b*, 1*b* and the abdominal border, these last dusted with silvered scales; between the end of 2 and the lobe some black and dark red scales; lobe orange and dark red edged with long black scales. Tails as above. Fringe of fore wing whitish chequered with brown at the end of veins, fringe of hind wing white. Expanse: 27–31 mm.

Male genital armature: Slide no. 3243, Albert Hill, Karamoja. Of the usual *Aphnaeus* type.

Female.—Very like the male from which it differs only in the following characters:

Wings, upperside: The blue suffusion of fore wings of a lighter and more vivid tinge and covers a larger area between the lower border of the cell. Vein 3 and the internal border, but does not reach the external border; in addition some blue scales at the base, middle and extremity of cell. *Underside.—Fore wing:* a small silver spot between 2 and 1, below the origin of 2; the silver spot situated between 4 and 3 is larger, slightly oval and nearly confluent with the anteterminal spot between 3 and 2. *Hind wing:* the dark red edging of the silver spots a little less apparent than in the male. Expanse: 33 mm.

Holotype ♂: UGANDA: Labwor Hill, Karamoja, iv. 1950 (*T. H. E. Jackson*), coll. T. H. E. Jackson.

Allotype ♀: Albert Hill, Mt. Kadam, Karamoja (*Dr. van Someren*), coll. van Someren.

Paratype 1 ♂: Same locality as the allotype (*Dr. van Someren*), coll. van Someren.

Aphnaeus adamsi sp. n. (Plates I and II, fig. 3, and Text-fig. 15).

Male.—Frons white with a double median line of carmine hair. Second joint of the palpi white below, with a lateral lining of carmine scales; third joint blackish. Antennae blackish with the tip of the club light yellowish.

Wings, upperside: Blackish-brown with shining greenish-blue markings which are placed as follows: *Fore wing:* Some greenish-blue scales at base and middle of cell, on the discoidals and in the postdiscal area between 5 and 3; a small spot between the origin of 3 and 2; a large spot between 2 and 1 and below 1, from the wing base to about 3 mm. from the external border. *Hind wing:* Basal subtriangular area shining greenish-blue, limited by veins 6 and 2, ceasing at about 3 mm. from the marginal border at the level of 6, at 1–5 mm. at the level of 2; marginal carmine spot between 2 and 1*b*; two blackish tails (extremities of 2 and 1*b*); abdominal border brownish furnished with long hair, brown near the base, reddish towards the anal angle. Fringe of both wings blackish-brown, yellowish along abdominal border. *Underside:* Yellow, slightly orange, very light, with silver and carmine markings as follows: *Fore wing:* A basal carmine spot; a sub-basal carmine spot beginning near the costa, reaching the lower border of the cell and enclosing both black and silver scales; a second transverse spot, like the preceding, from the costa to the origin of 2, a third covers the discoidals, encloses a silver centre and is confluent with a spot composed of black and carmine scales covering the base of the interspaces between 4 and 2; postdiscal series composed of three carmine spots dusted with some black scales, namely an oblong spot from the costa to 5, one much displaced towards the external border between 5 and 4 and the third in line with the first between 4 and 3; anteterminal series of carmine spots between the veins, nearly parallel to the external border, only the first two, between the costa and 6, farther from the external border; marginal border carmine, costa outlined with black from the second transverse spot to the apex, a scaly silvery zone, dusted with brown scales between vein 2 and the internal border. *Hind wing:* Three basal carmine spots, one at the beginning of the costa, one at the origin of 8, one at the beginning of the abdominal border: three carmine sub-basal spots, one between 8 and 7, one at the base of cell, the third long, with a silver centre, along 1*b*; an oblong spot, carmine with a silver centre on the discoidal; an irregular postdiscal series composed of a carmine spot between 8 and 7, of three confluent carmine spots between 7 and 4, a large carmine streak with a silver centre, V-shaped, from 4 to the abdominal border, its base confluent with the discoidal spot and its apex resting on vein 1*b*; anteterminal series of carmine spots, the first two isolated between 8 and 7, 7 and 6, the others confluent from 6 to the anal angle and touching the postdiscal series on vein 1*b*, the last spot of the anteterminal series between 1*b* and the anal angle, contains silver scales; marginal line carmine; a small silver marginal spot between the extremities of 2 and 1*b*. Fringe of both wings as above. Expanse 27–30 mm.

Male genital armature: Slide no. 3245, Bitje, Ja River, Cameroons. Of the type common to the genus, the anterior edge of the dorsum sinuate, the shape of the fultura inferior close to that of *Spindasis*.

Female: Differs from the male only in the following characters. *Wing shape:* apex of fore wing a little less acute, hind wing less drawn out at the anal angle, the marginal border more rounded. *Wings, upperside.—Fore wing:* The greenish-blue dot of the postdiscal area between 5 and 3 is lacking. *Hind wing:* The outer border of the greenish-blue area is slightly farther from the marginal border at the level of 6. *Wings, underside.—Hind wing:* The carmine spots of the postdiscal series between 7 and 4 are not confluent, the V-shaped streak is slightly interrupted after 1*b*. Expanse 33 mm.

Male holotype.—CAMEROONS: Bitje, Ja River, ix.1908, ex coll. Adams. British Museum (Nat. Hist.).

Female allotype: BELGIAN CONGO: Katako Komba, Sankuru, 16.xii.1951 (*Dr. M. Fontaine*), Musée du Congo Belge, Tervuren.

Paratype: One male, Djeke-Mbudi, Sankuru, 22.i.1953 (*Dr. M. Fontaine*), also in Musée du Congo Belge, Tervuren.

A. adamsi can be easily recognised by its carmine and silver markings on a light ground-colour.

Aphnaeus flavescens sp. n. (Plates I and II, figs. 4, 5, and Text-fig. 16).

Male.—Frons white with a median tuft of rufous hair. Second joint of palpi clothed with white adpressed hair, third joint blackish. Antennae (lacking in holotype). Thorax furnished below with long silky white hair. Legs clothed with white hair and scales.

Wings, upperside: Blackish-brown with metallic greenish-blue markings disposed as follows. *Fore wing:* Some greenish-blue scales at the base of cell, a small spot in its middle, another on the discoidals; longitudinal spots, of increasing length, situated between the veins 4 and 3, 3 and 2, 2 and 1, 1 and the internal border, the outer limit of these spots at about 4–5 mm. from thee xternal border, so leaving a wide marginal border of the ground-colour; some greenish blue scales below the lower border of cell. *Hind wing:* Small spots in the postdiscal zone, in the interspaces from vein 5 to between 2 and 1*b*; distal half of 1*b* outlined with metallic greenish-blue scales; tails black, white tipped; costal border brownish up to vein 6; abdominal border light brown, furnished with long whitish hair in the anal zone. Fringe blackish-brown at the base, whitish at the end; anal lobe edged with long black scales. *Underside:* Very light yellowish-white, nearly cream coloured with small faint silvery spots, widely encircled with black and dark red scales, arranged as follows: *Fore wing:* A round spot at the base of cell; an oblong transverse spot in its middle, a discoidal spot confluent with another which extends from the origin of 5 to 11;

postdiscal series very irregular, formed of six small spots: one between 10 and 9, one between 7 and 6, one displaced towards the base between 6 and 5, one strongly displaced towards the external border between 5 and 4, one between 4 and 3, one between 3 and 2; anteterminal series composed of a very small spot, with silver centre, between 9 and 8, two, larger, between 8 and 7, 7 and 6, a small spot between 6 and 5, two small dots of black and dark red scales between 5 and 4, 4 and 3, a spot also of black and dark red scales between 3 and 2, an indistinct shadow between 2 and 1; scaly, shining area between the base of 2 and the internal border. *Hind wing:* Three basal spots, one between the base of 8 and the upper border of the cell, one in the cell base, one near the base of the abdominal border; two dots of black and dark red scales along 1*b*, one at the base, the other below the origin of 2; two confluent spots cover the discoidals; a very irregular postdiscal series of eight spots: a large subcostal spot between 8 and 7, one much displaced towards the marginal border between 7 and 6, one nearer the extremity of cell between 6 and 5, one again displaced towards the marginal border between 5 and 4, two confluent between 4 and 2, an oblong spot below 2 and another directed towards the base of the wing between 1*b* and 1*a*; subterminal series formed of a small apical spot between 8 and 7, a larger one between 7 and 6, some black scales between 6 and 3, a small spot between 3 and 2, a silver streak from 2 to the abdominal border; lobe blackish with some bluish-white scales; tail at end of 1*b* rufous at the base, then black, white tipped. In both wings, marginal line blackish, fringe brown at the base, then white. Expanse: 29 mm.

Male genital armature: Slide no. 3244, Limbe, Nyasaland. Of the usual *Aphnaeus* type.

Female.—Differs from the male only by the larger expanse and the reduced size of the metallic greenish-blue spots of the fore wing upperside. Expanse: 35 mm.

Holotype ♂, NYASALAND: Limbe.

Allotype ♀: NYASALAND: Chintechi, i–v.1924 (*T. H. Lloyd*), both specimens, ex coll. Joicey, are in the British Museum (Nat. Hist.).

By its creamy-coloured underside, *flavescens* differs strikingly from all the other *Aphnaeus* species.

Aphnaeus hutchinsoni Trimen (Text-fig. 17).

A. hutchinsoni Trimen, 1887, *South African Butterflies* **2** : 148.
A. zanzibarensis Smith, 1889, *Ann. Mag. nat. Hist.* (6) **3** : 136.

Male genital armature.—Slide no. 1612, Zanzibar. Of the usual *Aphnaeus* type; the penis is short and massive, the fultura inferior is shield-shaped, rather like that of *Spindasis.*

The ground-colour of the underside of *hutchinsoni* is as variable as that of *orcas.* Of the holotype, Trimen says: " dull pale ochreous yellow "; Smith defines that of *zanzibarensis* as " brown, paler at the outer margin "; Desmond P. Murray (*South African Butterflies* : 82) speaks of " dull olivaceous "; Aurivillius (*Sietz* **13** : 409) of " olivenfarbig". In many specimens from Pretoria, Delagoa Bay and Zanzibar, the carmine red circles which surround the silver spots are very wide and wholly invade the ground-colour, so that the underside appears to be of a dark violaceous-red, nearly amaranthine in the male. In females from Zanzibar the underside colour remains lighter, yellowish-ochreous, but the upperside already shows a trace of the reddish marginal border, characteristic of the race *drucei* Neave.

Habitat: CAPE DISTRICT, NATAL, TRANSVAAL, DELAGOA BAY, ZANZIBAR, SOUTHERN RHODESIA (according to R. Stevenson).

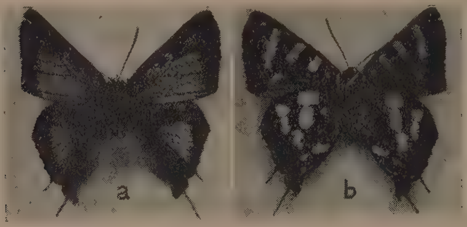


FIG. 18.—*Aphnaeus nyanzae* sp. n. ♂. *a*, upperside, *b*, underside.

A. hutchinsoni drucei Neave.

A. drucei Neave, 1904, *Novit. Zool.* **11** : 338, pl. i, fig. 6.

Differs from the nominate form in the following characters :

Male.—Wings, upperside. Fore wing : Marginal border ferruginous red, about 1–5 mm. wide, from the apex to the tornus. *Hind wing :* Marginal border from 6 to 1*b* also ferruginous red. *Underside :* Ground colour plain leather brown, no submarginal reddish line in fore or hind wing. (The male genital armature is identical to that of typical *hutchinsoni*)

Female.—Like the male, the underside silver spots sometimes reduced in size.

A. drucei has been described as a distinct species, but without any doubt it is but a local form of *hutchinsoni* for, as mentioned above, some females from Zanzibar are transitional in their upperside colour.

Habitat : Described from TANGANYIKA ; also known from Kima, Kenya (*van Someren, T. H. E. Jackson*), Elgon, Karamoja district, Uganda (*T. H. E. Jackson*). The early stages of *A. hutchinsoni drucei* have been described by T. H. E. Jackson (1937, *Trans. R. ent. Soc. Lond.* **86** : 216, 217).

Thierry Mieg (*Naturaliste* **1904** : 140) erected the genus *Paraphnaeus* for *hutchinsoni* Trimen, giving as the only generic character the rounded shape of the underside spots. In my opinion, this generic name should be considered as a mere synonym of *Aphnaeus*.

Aphnaeus asterius subspecies

I have recently received a pair of *A. asterius*, collected in November 1953, by Mr. T. H. E. Jackson and Dr. van Someren at Sango Bay, Katera, Uganda. These specimens seem to belong to a distinct Eastern subspecies, characterized as follows :

Male.—wings, upperside : Russet blackish-brown, without any trace of greenish-blue patches ; lobe of hind wing reddish-orange, tails orange and black. *Underside :* Reddish-orange, all the markings reduced in size, black with only a few silver scales in their centre. Expanse : 23 mm.

Genital armature : Identical to that of the nominate form.

Female wings.—Upperside : Uniform blackish-brown, without any trace of violet-blue patches ; some whitish scales in the lobe ; tails black, white tipped. *Underside:* Deep orange, a little lighter than in the male, all the markings reduced in size, as in the male. Expanse : 30 mm.

Only this pair of specimens has been found ; the study of more material is necessary before deciding if this form should be considered a geographical race.

PLATES I AND II

1. *A. erikssoni barnesi* subsp. n. ♂.
S. Rhodesia, Umtali, 18.x.1924.
E. W. Lannin.

2. *A. erikssoni rex* Aurivillius ♀.
Nyasaland, Mlanje, 15.x.1913,
2,300 ft. S. A. Neave.

3. *A. adamsi* sp. n. ♂.
Type
Bitje, Ja River, Cameroons, Sept.,
1908.
Adams Bequest.
Stempffer diss. 3245.

4. *A. flavescens* sp. n. ♂.
Type
Limbe, Nyasaland.
Joicey Bequest.
Stempffer diss. 3244.

5. *A. flavescens* sp. n. ♀.
Type
Chintechi, Nyasaland, Jan.–May,
1924. T. H. Lloyd.
Joicey Bequest.

6. *A. affinis affinis* Riley ♂.
Chanteti R., Solwezi, 8–17.
Stempffer diss. 3237.

7. *A. affinis seydeli* Berger ♀.
Type
Lukunga, 7.xi.1915.
(L. Berger det. 1949. *Aph. elisabethae* Berger ♀).
Stempffer diss. 3410.

8. *A. erikssoni erikssoni* Trimen ♂.
Katanga, Belgian Congo.
Joicey Bequest.

9. *A. jacksoni* sp. n. ♂.
Type
Labwor Hills, Karamoja, T. H. E.
Jackson.
Stempffer diss. 3241.

10. *A. jacksoni* sp. n. ♀.
Type
Mt. Kadam(?) Karamoja, iv.1950.
van Someren.

11. *A. orcas* f. *paupera* f. n. ♂.
Type
Afrique, Lulua-Sankuru, Haut-Kasai,
Landbeck. 1902–04. ex Oberthür
Coll.

12. *A. orcas* f. *paupera* f. n. ♀.
Type
Uganda Prot., between Seziwa R.
and Kampala, 3500–3750 ft. Aug.
27–31, 1911. S. A. Neave.

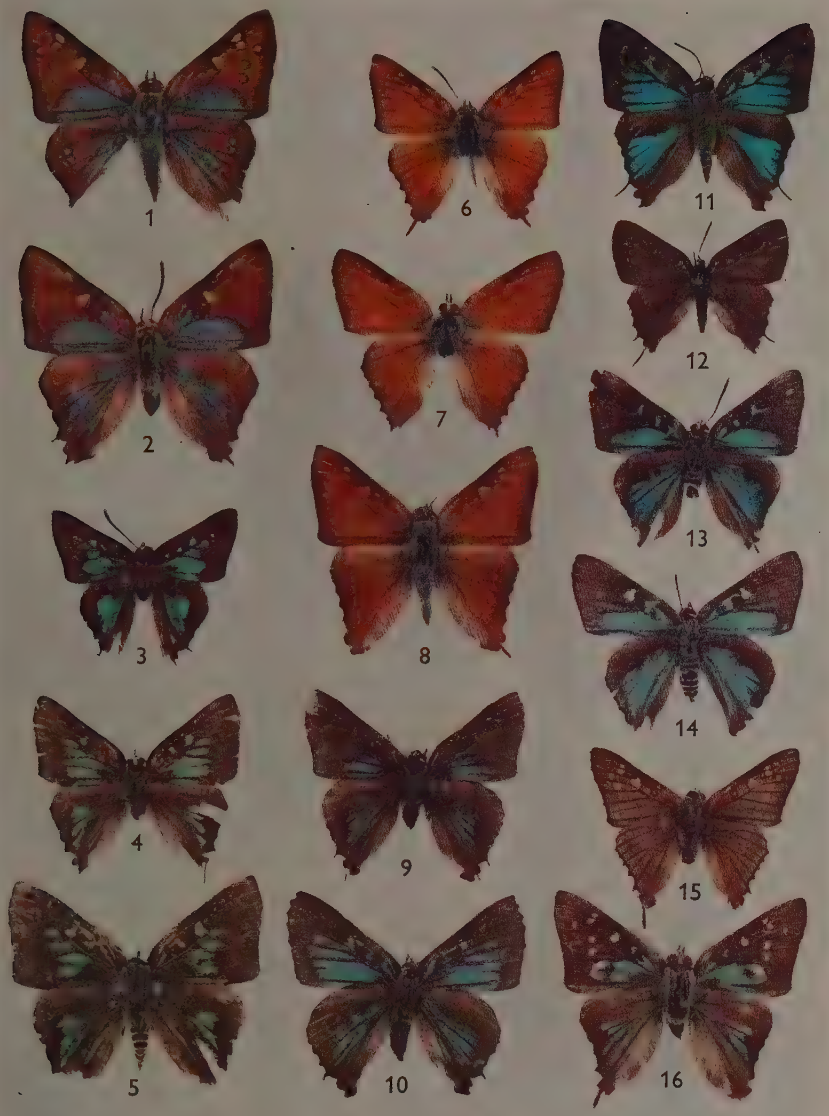
13. *A. coronae vansomereni* subsp. n. ♂.
Labwor Hills, Karamoja. April,
1950. T. H. E. Jackson.

14. *A. coronae coronae* Talbot ♀.
Type
Toror, Karamoja. April, 1950.
T. H. E. Jackson.

15. *A. neavei* Beth. Baker ♂.
Garsen, Kenya, July, 1940. T. H. E.
Jackson.
Stempffer diss. 3203.

16. *A. questiauxi* Aurivillius ♀.
N.E. Rhodesia, Sontola R., Luena
Dist. 29.viii.1904. R. L. Harger.
Stempffer diss. 3239.

Plate 1.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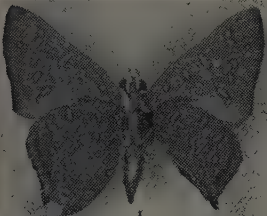
H. Stempffer.

The genus *Aphnaeus* Hubner.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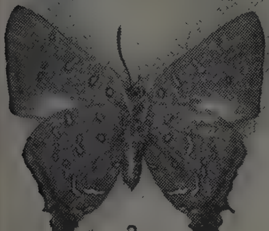
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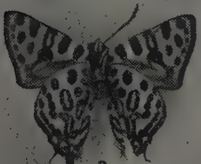
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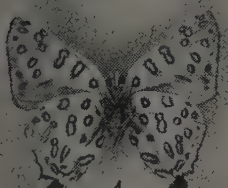
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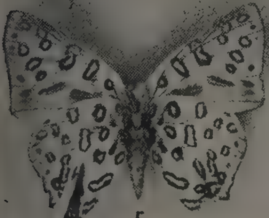
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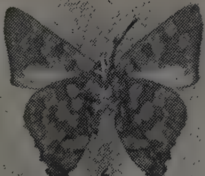
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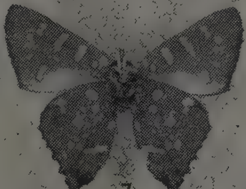
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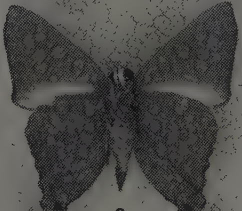
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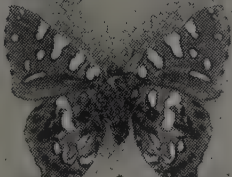
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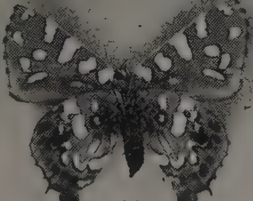
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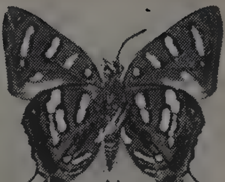
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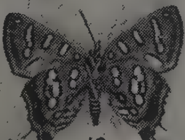
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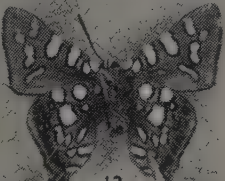
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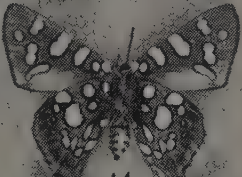
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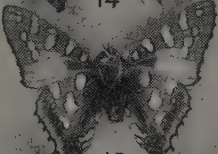
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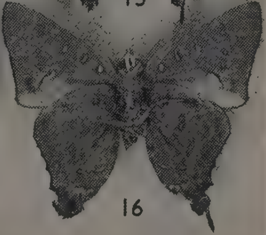
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ERRATA.

p. 2, line 5. For " Krombien " read " Krombein."
p. 9, centre of chart. For " *Ragigaster* " read " *Rhagigaster*."
p. 47, line 5. For " sera " read " sere."
p. 100, couplet 14, for " **Pleuvovittata** " read "**Pleurovittata.**"
p. 267, line 6, for " *laeus-coerulei* (Tillyard), 1921, " read " *lacus-coerulei* (Tillyard), 1933."
p. 267, REFERENCES. Add " LESTAGE, J. A., 1935*a*, Contribution à l'étude des Ephéméroptères. XII. Les composantes australiennes et néo-zélandaises du Groupe Siphlonuridien. *Bull. Ann. Soc. ent. Belg.* **75**: 346–358."
For " STEPHEN, J. F." read " STEPHENS, J. F."
p. 290, line 5 from bottom, for " *Orydiscus* " read " *Oxydiscus*."
p. 303, line 23, for " Stratiomydae " read " Stratiomyidae."